Generic recircumscription in the Loxocarpinae (Gesneriaceae), as inferred by phylogenetic and morphological data

New generic recircumscription of the Loxocarpinae (Gesneriaceae), as inferred by phylogenetic and morphological data

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Abstract

The Loxocarpinae, also known as the "*Boea* group", are the subtribe of Gesneriaceae which includes *Boea* and a number of segregated genera and close relatives. This group currently comprises over 200 species in 15 genera. Here we present the most up-to-date phylogeny, covering all the genera known to belong to the group, based on Bayesian Inference and Parsimony of the nuclear ITS and the plastid regions *trnL-trnF* (intron and spacer) and *ndhF*- $trnL^{UAG}$ (spacers). The results show discrepancies between the current generic delimitation in the subtribe and the clades delineated by the phylogeny. As a result *Boea*, *Damrongia*, *Streptocarpus* and *Paraboea* are recircumscribed in an attempt to establish a more natural classification and a number of new combinations are made. The new genus *Middletonia* is described.

Keywords: *Boea*, *Damrongia*, *Paraboea*, Southeast Asia, *Streptocarpus*.

Phylogeny of Loxocarpinae.

Introduction

The Gesneriaceae are a large family with an estimated 3500 species in 147-150 genera (Stevens, 2001 onwards; Skogg & Boggan, 2007; Möller & Clark, 2013;Weber & al., 2013), distributed mostly in the tropics and subtropics, with some outliers in the temperate areas of both hemispheres (Weber, 2004). The subject of this investigation is the group formerly referred to informally as the "advanced Asiatic and Malesian Gesneriaceae with twisted fruit" (Möller & al., 2009) and now formally classified as the subtribe Loxocarpinae, part of the tribe Trichosporeae, subfamily Didymocarpoideae (Weber & al., 2013). It is also informally known as the '*Boea* group' (Möller & al., 2009; Puglisi, 2014).

The Loxocarpinae are found throughout Southeast Asia, reaching Australia and the Solomon Islands, and are characterised by having a predominantly twisted capsule. However, in some genera all the species have a 'straight' fruit, with valves not twisting (e.g. *Loxocarpus* R.Br.), and in other genera there are species with a twisted fruit and species with a straight fruit (e.g. *Paraboea* (C.B.Clarke) Ridl., Fig. 1).

The first genus in the subtribe described to accommodate twisted-fruited species was *Boea* Comm. ex Lam. *Boea* grew larger, and became rather heterogeneous, as more species with the same fruit type were discovered and were described in the genus. Progressively, the majority of the species was then transferred to other genera, many of which were directly segregated from *Boea*, in order to establish morphologically distinct units.

Key publications, in which many species of *Boea* were described, are the works by Brown (1839, 1840) and Clarke (1883). The most important recent work on the *Boea* group is that by Burtt (1984), in which the generic concepts formed around a twisted-fruited *Boea* and a straight-fruited *Paraboea* were profoundly modified with new generic concepts based on indumentum type rather than on the fruit twisting. This change led to a large number of species being transferred from *Boea* to *Paraboea*. Later, the new genera *Kaisupeea* B.L.Burtt (Burtt, 2001), *Senyumia* Kiew, A.Weber & B.L.Burtt, *Spelaeanthus* Kiew, A.Weber & B.L.Burtt and *Emarhendia* Kiew, A.Weber

& B.L.Burtt (Kiew & al., 1997), were created to accommodate the few remaining doubtful species of *Boea* and *Paraboea*.

The study by Möller & al. (2009) was the first phylogenetic investigation focusing on the tribe Trichosporeae (then referred to as Didymocarpoid Gesneriaceae). In a subsequent study, Möller & al. (2011) expanded their sampling and confirmed that the straight-fruited genera *Chirita* Buch.-Ham. and *Henckelia* Spreng. were both polyphyletic and that taxa of both were to be found in the *Boea* group. Weber & al. (2011), Yao (2012) and Middleton & al. (2013) focused on these problematic genera and, as a result, *Chirita* was split into five genera, including *Damrongia* Kerr ex Craib within the *Boea* group, comprising a few species from the former *Chirita* sect. *Chirita*. Likewise, *Henckelia* was split into three genera, including *Loxocarpus* in the *Boea* group (formerly *Henckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burtt). Puglisi & al. (2011a) also examined relationships within the *Boea* group, focusing on the genera *Paraboea*, *Trisepalum* C.B.Clarke and *Phylloboea* Benth., resulting in them all being synonymised under *Paraboea* (following conservation of the name by Middleton & al., 2010), by far the largest genus in the Loxocarpinae.

The aims of this new study are to reconstruct the molecular phylogenetic tree for the entire subtribe Loxocarpinae, to test whether the current classification is in agreement with the phylogenetic structure of the group, to identify robust phylogenetic entities suitable for a redefinition of the generic limits, and to propose a new generic classification accordingly.

Materials and methods

In this study, 140 ingroup accessions belonging to 110 taxa of Loxocarpinae were sequenced, and all the genera recognised in the subtribe were included. The outgroup consisted of six accessions of the closely related subtribes Didissandrinae, Didymocarpinae and Streptocarpinae (Weber & al., 2013), represented by two taxa of *Didissandra* C.B.Clarke, *Codonoboea* Ridl. and African *Streptocarpus* Lindl. respectively.

The material used in the analyses consisted of silica gel-dried leaves samples with the exception of the sample called "*Boea* sp.", which was taken from a herbarium specimen

(*Hoogland 5129*, CANB herbarium). Generic types have been included for all the genera with the exception of *Boea* and *Ornithoboea* Parish ex C.B.Clarke, for which no material suitable for DNA extraction was available. Information on the accessions, including collection data, repository of the vouchers and GenBank numbers, is available as supplemental material.

Total genomic DNA was extracted following a modified version of the cetyltrimethyl ammonium bromide (CTAB) method by Doyle & Doyle (1987), with no further purification.

The markers used in the phylogenetic analyses were chosen based on previous work on the Didymocarpoideae (e.g. Atkins & al., 2001; Bramley & al., 2004; Clark & al., 2009; Möller & al., 2009, 2011; Puglisi & al., 2011a, 2011b; Puglisi, 2014). These were the nuclear ITS and the plastid regions *trnL-trnF* (including both the *trnL* intron and the *trnL-trnF* spacer) and *ndhF-trnL*^{UAG} (*ndhF-rpl32* and *rpl32-trnL*^{UAG} spacers).

The PCR of the ITS and *trnL-trnF* regions followed an optimised recipe already tested in previous studies (Puglisi & al., 2011a, 2011b). The 20 µl reaction contained 2 µl 2 mM dNTPs, 2 µl 10x NH_4 buffer, 0.6 µl 25 mM $MgCl_2$, 2µl each 10 µM forward and reverse primer, 0.4 µl 0.4% BSA, 0.4 µl Biotaq polymerase (Bioline), 1 µl DNA template and 9.6 µl dH_2O. In some cases, TBT-PAR was employed as recommended by Samarakoon & al. (2013) and it seemed to have a positive effect on problematic PCRs. The 20 µl PCR reaction mix containing TBT-PAR was: 2 µl 2 mM dNTPs, 2 µl 10x NH_4 buffer, 0.6 µl 25 mM $MgCl_2$, 2 µl each 10 µM forward and reverse primer, 4 µl 5x TBT-PAR, 0.4 µl Biotaq polymerase (Bioline), 1 µl DNA template and 6 µl dH_2O. The primers used to amplify the ITS were 5P and 8P (Möller & Cronk, 1997). Occasionally, the internal primers 2G and 3P (Möller & Cronk, 1997) were used when the sequencing signal strength was low. The thermocycle settings used in the PCR were: 94°C for 3', 30× [94°C for 1', 55°C for 1', 72°C for 1.5'], 72°C for 5', 10°C forever. The *trnL-trnF* region was amplified using the universal primers c, d, e and f (Taberlet & al., 1991). While this intron-spacer region is generally amplifiable with just the external primers c and f, a number of samples proved problematic and needed several adjustments to the PCR reaction and thermocycle settings. However, none of these variations appeared optimal or widely applicable. The following PCR thermocycle settings were used: 94°C

for 4', 35× [94°C for 45", 55°C for 45", 72°C for 3'], 72°C for 10', 10°C forever. The primers used for the amplification of the *ndhF-trnL*^{UAG} were ndhF, rpl32F, rpl32R and trnL^{UAG} (Shaw & al., 2007).

The two spacers *ndhF-rpl32* and *rpl32-trnL*^{UAG} were tentatively co-amplified or, when necessary, treated individually. The thermocycle settings used in the PCR of the entire region were 80°C for 5', 30× [95°C for 1', 50°C for 1', 65°C for 1' 7" with ramp of 0.3 C/sec, 72°C for 2'], 72°C for 5', 4°C forever. Individual spacers, instead, followed the thermocycle 80°C for 5', 30× [95°C for 1', 50°C for 1', 65°C for 1'7" with ramp of 0.3 C/sec, 65°C for 4'], 65°C for 5', 4°C forever.

PCR products were stained with SYBR Safe (Invitrogen) and checked by electrophoresis on 1% agarose gel. Successful PCR products were purified with ExoSAP-IT (Affymetrix), following the manufacturer's protocol. Sequencing PCRs were 1/8 reactions with BigDye Terminator v.3.1 (Applied Biosystems). The thermocycle was: 25× [95°C for 30", 50°C for 20", 60°C for 4'], 4°C forever. Sequencing products were processed at the GenePool laboratory of the University of Edinburgh on an ABI3730 DNA Analyser (Applied Biosystems). Sequences were edited in Sequencher v.4.7 (Gene Code Corporation) and aligned manually in Mesquite v.2.74 and v.2.75 (Maddison & Maddison, 2010, 2011).

Given the relatively low number of sequences available for the *ndhF-trnL*^{UAG} plastid DNA region, two different datasets were analysed: the "2-markers" dataset with 142 accessions, including only ITS and *trnL-trnF* data, and the "3-markers" dataset with 68 accessions, but with the additional contribution of the *ndhF-trnL*^{UAG} region (Table 1). Four of the accessions included in the 3-markers dataset were not analysed in the larger 2-markers dataset, due to the low quality of some sequences, especially the *trnL-trnF*, and the simultaneous presence in the matrix of other accessions of the same species with more reliable sequences.

Parsimony analyses were run in PAUP* v.4.0b10 (Swofford, 2003) on unordered and unweighted characters with the following settings: heuristic search running over 100,000 stepwise random addition replicates, with two trees held at each step; tree bisection reconnection (TBR) branch swapping algorithm with steepest descent and MulTrees options enabled; MaxTrees setting fixed at 1,000,000. The resulting parsimonious trees were filtered to retain the 'best score' trees only. Topological

support for the phylogenies was estimated by bootstrap analyses. These were run with 10,000 pseudo-replicate samples, following the parsimony criterion and the following heuristic search settings: stepwise random addition, one replicate and TBR on; steepest descent and MulTrees options disabled.

Evolution models for Bayesian Inference were inferred in jmodeltest2 (Guindon & Gascuel, 2003; Darriba & al., 2012) according to the Akaike Information Criterion (AIC - Akaike, 1974). While the plastid markers *trnL-trnF* and *ndhF-trnL*^{UAG} were not partitioned, thus assuming a uniform evolutionary rate across the regions, two distinct elements were identified within the nuclear ITS: the highly conserved *5.8S* gene and the combined, highly variable spacers ITS1 and ITS2. Sequences and models were analysed for Bayesian Inference in MrBayes v.3.2.2 (Ronquist & Huelsenbeck, 2003; Ronquist & al., 2011). Preliminary tests were run to help choose the most suitable parameter settings. The number of generations was fixed at 10 million, with a sample frequency of 1000 and a burn-in of 2000, for both matrices. The Bayesian analyses were run on the CIPRES Science Gateway V 3.3 (Miller & al., 2010). The output trees were edited in FigTree v.1.3.1 (Rambaut & Drummond, 2009).

Results

The combinability of the different partitions was assessed through preliminary individual Bayesian analyses (not shown). Overall, the resulting trees did not highlight any topological conflict, with the exception of minor discrepancies generated by the low resolution at the backbone of the trees and among the branches subtending the genera *Loxocarpus*, *Emarhendia* and *Orchadocarpa* Ridl. However, since the clades defined by the phylogenies remained consistent, the partitions were combined for analysis.

The outputs of the Parsimony and Bayesian Inference of the two datasets, 2-markers and 3-markers, have been summarized in four consensus trees (strict for Parsimony, 50% majority rule for Bayesian Inference, all presented as electronic supplement). The trees do not have fully matching topologies especially towards the backbone, but consistently outline the same well-defined seven clades (Fig. 2), which are the focus of this study. These clades all receive maximum support in the Bayesian 3-markers analysis, as do all except clade 3 in the Bayesian 2-markers analysis (0.64 posterior probability). Clade 3 has no support in either Parsimony analysis. Of the other groups,

179 all but clade 4 receive 100% bootstrap support in the Parsimony 3-markers analysis,
180 whereas in the Parsimony 2-markers analysis clades 4 and 6 receive less than 95%
181 support (Table 2).

182 The first clade to diverge within the ingroup is clade 1 (Fig. 2), formed by a group of
183 species ascribed to *Paraboea*, specifically *P. monticola* Triboun & D.J.Middleton which
184 is sister to *P. evrardii* (Pellegr.) B.L.Burtt and *P. multiflora* (R.Br.) B.L.Burtt. The
185 position of this group, with respect to the remaining ingroup taxa and the core of
186 *Paraboea*, is consistent in all the trees generated in this study, although is statistically
187 supported only by the Bayesian analyses.

188 With an increased sampling since Puglisi & al. (2011a), all the remaining species of
189 *Paraboea* form a strongly supported monophyletic group (hereafter referred to as
190 *Paraboea sensu stricto*), i.e., clade 7.

191 Similarly, *Boea* is polyphyletic, with species spread across clades 2, 3 and 6. Clade 2
192 comprises *B. geoffrayi* Pellegr., *B. hygrometrica* (Bunge) R.Br., *B. philippensis*
193 C.B.Clarke and a new species (*Boea* sp. nov.). The relative position of *Boea geoffrayi* is
194 not stable, as it appears as either sister to the new species (2-markers dataset) or to *B.*
195 *philippensis* (3-markers dataset).

196 Clade 3 contains all the examined species of *Loxocarpus*, nested within which are
197 *Emarhendia* and *Orchadocarpa*, plus a well-supported subclade (bootstrap 97-100%,
198 posterior probability 1) comprising *Senyumia*, *Spelaeanthus* and the Australasian
199 species of *Boea*. In *Boea*, the Australian *B. hygroscopica* F.Muell. is sister to the
200 accessions from Papua New Guinea, *B. lawesii* H.O.Forbes and *Boea* sp. Sister to this
201 subclade in most analyses (the 2-marker parsimony analysis is equivocal) is a clade of
202 *Loxocarpus* which includes *L. rufescens* (C.B.Clarke) B.L.Burtt, *L. sericiflavus* (Kiew
203 & Banka) T.L.Yao, *L. holttumii* M.R.Hend. and related species. A second clade of
204 *Loxocarpus* is formed by the accessions of *L. incanus* R.Br. and is most closely related
205 to *Orchadocarpa*. The remaining accessions of *Loxocarpus*, *L. argenteus* B.L.Burtt, *L.*
206 *violoides* (C.B.Clarke) T.L.Yao, *L. verbeniflos* (C.B.Clarke) B.L.Burtt and *L. repens*
207 B.L.Burtt, form a further, well supported clade. The affinities of *Emarhendia* are not
208 entirely clear.

The remaining *Boea* species, *B. clarkeana* Hemsl., is nested within *Damrongia* in clade 6 in all the analyses, and is sister to *D. trisepala* (Barnett) D.J.Middleton & A.Weber and *D. cyanantha* Triboun. Likewise, *Streptocarpus sumatranus* B.L.Burtt is consistently nested inside *Damrongia* and is likely related to *D. lacunosa* (Hook.f.) D.J.Middleton & A.Weber or *D. fulva* (Barnett) D.J.Middleton. All these species together form a well-supported clade, which is sister to *Streptocarpus orientalis* Craib, completing clade 6. Clade 6 is strongly supported as sister to clade 5, which corresponds to a clearly monophyletic *Somrania* D.J.Middleton. Within *Somrania*, *S. albiflora* D.J.Middleton is sister to *S. lineata* D.J.Middleton & Triboun plus *S. flavida* D.J.Middleton & Triboun.

Clade 4 is formed by *Kaisupeea* and *Rhabdothamnopsis* Hemsl. (the latter genus not represented in the 3-markers dataset) as sister genera to *Ornithoboea*. In *Kaisupeea*, the relationships between the three species remain unclear, with poor support for the placement of *K. cyanea* B.L.Burtt. *Ornithoboea* receives maximum support as a monophyletic genus.

Discussion

Our analyses reveal that the Loxocarpinae comprise a number of well-supported clades, with the exception of clade 3, and also reveal that many genera are not monophyletic (*Boea*, *Damrongia*, *Loxocarpus*, *Paraboea* and *Streptocarpus*). Among the genera with more than one species, only the monophyly of *Ornithoboea*, *Somrania* and *Kaisupeea* is supported. However, relationships between many of these clades are poorly resolved or supported, providing only limited information about higher level relationships within the subtribe. Relationships involving *Loxocarpus*, *Emarhendia* and *Orchadocarpa* within clade 3 are particularly complex.

Boea.--- This study confirms the polyphyly of *Boea* already shown by Möller & al. (2009, 2011). Six out of 14 species were included in the analyses. They are found in three different clades (2, 3 and 6): *Boea clarkeana* (Fig. 3: 6c) is nested in *Damrongia* (clade 6), whereas *B. hygroscopica* (Fig. 3: 3f), *B. lawesii* and an unnamed species form a clade with *Senyumia* (Fig. 3: 3d) and *Spelaeanthus* (Fig. 3: 3e), nested within *Loxocarpus* (clade 3). The remaining four species examined form a clade on their own

(clade 2, Fig. 3: 2). These results indicate that *Boea*, already greatly reduced in size by the removal of several segregate genera and the realignment with *Paraboea*, is not tenable in its current delimitation and should be split. Morphological characters, such as the shape of the corolla, also support a formal separation. The type species of *Boea*, *B. magellanica* Comm. ex Lam., from Papua New Guinea and the Solomon Islands, was not examined here, but has the same corolla morphology as the other members of the Australasian group, especially *Boea lawesii*: the flower has a flat-faced, unevenly coloured corolla and the stamens are exserted; the filaments are bent and they appear bright yellow and fleshy. Conversely, the corolla of all the species forming clade 2 is uniformly lilac to blue, obliquely campanulate with a ventricose tube, reflexed upper lobes and a broad throat; the stamens are included in the throat, have slender filaments and the anthers are erect (Fig. 3: 2). Under the new circumscription suggested here, the name *Boea* remains with the Australasian group (*B. magellanica*, *B. hygroscopica*, *B. lawesii*, etc.), whereas clade 2 acquires the resurrected name *Dorcoceras* Bunge (1832), coined for *Dorcoceras hygrometricum* Bunge. The hitherto inclusion of the species of *Dorcoceras* within *Boea* is a relic of the very broad generic concept adopted by Clarke (1883) which neither Schlechter (1923) nor Burtt (1984) effectively resolved. The resurrected *Dorcoceras* includes the four Southeast Asian species of *Boea* with a campanulate corolla: *B. geoffrayi*, *B. hygrometrica*, *B. philippensis* and *B. wallichii* R.Br. The new combinations are provided below.

Boea clarkeana, instead, is transferred to *Damrongia*, based on the results of the phylogenetic analysis and its morphological similarity to *D. trisepala* (Fig. 3: 6b). There are also substantial differences between *Boea clarkeana* and the existing species of *Damrongia*, the most obvious of which are in the fruit. *Boea clarkeana* has an orthocarpic, twisted capsule that bears little resemblance to the plagiocarpic, straight fruit of the other *Damrongia* species. However, *Paraboea* (Puglisi & al., 2011a and see below) and *Ornithoboea* (Scott & Middleton, 2014) also contain species with twisted and species with non-twisted capsules, indicating that this character is variable within genera, and hence not a good argument against transferring *Boea clarkeana* to *Damrongia*.

Paraboea.--- *Paraboea* was found to be non-monophyletic, with clade 1 forming a group separate from all the other species (Fig. 2). *Paraboea s.s.* (clade 7, Fig. 3: 7) is monophyletic with high statistical support and the same overall structure as found by Puglisi & al. (2011a). The first subclade to diverge includes all species with a calyx divided into five equal parts that are found north of the Isthmus of Kra in the Thai Peninsula. Of the two other sister subclades, one comprises species formerly placed in *Trisepalum* and *Phylloboea*, and is characterised morphologically by a strongly bilabiate calyx; the other, instead, comprises species with a calyx divided into five equal parts and distributed south of the Isthmus of Kra and in Malesia.

Clade 1 possesses characters typical of *Paraboea*, such as the interwoven indumentum on the lower surface of the leaves, the flat-faced corolla and the twisted capsules. However, these plants also have stamens with free, erect anthers opening upwards, with the apices of the anthers parallel to the axis of the flower. The species of *Paraboea s.s.*, conversely, have anthers with the apex rotated towards the gynoecium, coherent, divergent and opening along the median line. The gynoecia also differ, as in clade 1 there is an indumentum of minute white, greenish or yellow glands on the ovary and the capsule which is absent in clade 7. The clear phylogenetic and morphological distinction of this group from the rest of *Paraboea* supports the segregation of a new genus, *Middletonia* C.Puglisi (Fig. 3: 1).

It should be noted that the sample of *Paraboea multiflora* in Puglisi & al. (2011a), which formed a monophyletic clade with the core *Paraboea* species, was misidentified. The voucher (*Wen 2010-01*, collected in Guangdong, China) could not be located but a new specimen said to be from the same locality and of the same species by the original collector has been identified as *Paraboea cf. dictyoneura* (Hance) B.L.Burtt, which is morphologically similar to the species in its clade and not to *P. multiflora*. The sample was omitted from the analyses presented here.

Streptocarpus.--- *Streptocarpus* is an Afro-Madagascan genus with c. 140 species, first described in 1828. Due to the presence of a twisted capsule, Franchet (1899), Craib (1911, 1919) and Burtt (1962) decided to ascribe to this genus some Asian plants which did not have a better alternative placement. There are currently three species of *Streptocarpus* in Asia: *S. burmanicus* Craib from Burma, *S. orientalis* from Thailand

and *S. sumatranus* from West Sumatra (Indonesia). Despite the carpological similarity, Möller & al. (2009), Puglisi (2014) and the present study all show that *Streptocarpus orientalis* does not form a monophyletic group with the other species of the genus (represented by the African *S. rexii* and *S. glandulosissimus* in the present study). Puglisi (2014) and the present study additionally show that *Streptocarpus sumatranus* does not form a monophyletic group either with the African species or with *S. orientalis*.

In the present study, *Streptocarpus sumatranus* is nested within *Damrongia*. When he described it, Burtt (1962) was unable to place it in any existing Southeast Asian genus of Gesneriaceae and opted, cautiously, for *Streptocarpus* because of its caulescent habit, the narrowly campanulate corolla and the twisted capsule. Moving *Streptocarpus sumatranus* into *Damrongia* is currently the best option, or at least the only viable option, given its current, untenable position as a species of *Streptocarpus*. This inclusion deeply alters the morphological characterisation of *Damrongia*, especially through the introduction of the caulescent habit in the genus. A twisted fruit has already been introduced into *Damrongia* by the inclusion of *Boea clarkeana*, incidentally a species also formerly ascribed to *Streptocarpus* (Hilliard & Burtt, 1971).

Streptocarpus orientalis is sister to *Damrongia* (incl. *Boea clarkeana* and *Streptocarpus sumatranus*, Fig. 3D). Its inclusion in *Streptocarpus* is clearly erroneous and the species requires a more appropriate generic placement. As the expanded *Damrongia*, including *Boea clarkeana* and *Streptocarpus sumatranus*, already possesses morphological characters such as the twisted capsule, caulescent habit and chiritoid stigma (two-lipped stigma with the upper lip strongly reduced and the lower bilobed), which are characters also present in *S. orientalis*, the most appropriate course of action is to place *S. orientalis* in *Damrongia*, rather than in a separate genus. Although no sample of *Streptocarpus burmanicus* was available for DNA extraction, its morphology suggests this species to be very closely related to *S. orientalis*. With these changes, the distribution of *Damrongia* becomes much wider, from China to Sumatra.

Loxocarpus.--- *Loxocarpus* was found to be non-monophyletic in this and previous phylogenies (Yao, 2012; Puglisi, 2014), forming three distinct, well-supported clades.

Mixed in with these, and together forming clade 3, are *Orchadocarpa*, *Emarhendia* and the *Boea*/*Spelaeanthus*/*Senyumia* subclade, but relationships among these lineages are not fully resolved.

One *Loxocarpus* clade contains all the accessions of the type species of the genus, *Loxocarpus incanus*, including *L. incanus* var. *sekayuensis* (Banka & Kiew) T.L.Yao. In the 2-markers trees, the separation of *Loxocarpus incanus* var. *sekayuensis* from *L. incanus* var. *incanus* does not receive strong support. Further investigation of this species is needed as perhaps the identifications were not accurate at the varietal level. A second clade of *Loxocarpus*, including e.g. *L. violoides* (C.B.Clarke) T.L.Yao, is entirely composed of species from Borneo and is morphologically heterogeneous in that it includes one species, *L. argenteus* B.L.Burtt, with a campanulate corolla, in contrast to the other members of the group, all with flat-faced corollas (Yao, 2012). The third *Loxocarpus* clade is entirely made of species with a campanulate corolla, comprising *L. rufescens* (C.B.Clarke) B.L.Burtt from Borneo and species from the Malay Peninsula. This clade is sister to the *Senyumia*/*Spelaeanthus*/*Boea* alliance in all the analyses, but this relationship receives significant support only in the 3-markers Bayesian Inference. Nevertheless, *Loxocarpus* is clearly paraphyletic and perhaps best split into three different genera, since the morphologies of *Boea*, *Senyumia* and *Spelaeanthus* are too different to encourage the synonymisation into a large genus encompassing the entire clade 3 (Fig. 3: 3). However, the geographical and morphological ranges present in *Loxocarpus* remain relatively poorly sampled, and these, plus the incomplete resolution of clade 3, make the proposition of formal taxonomic changes premature. Hence *Loxocarpus* is left unaltered, until further studies provide more data.

Patterns of diversity.--- Gesneriaceae present several fruit types: fleshy or dry berries and capsules, these orthocarpic or plagiocarpic, cylindrical or conical and varying greatly in length and mode of dehiscence (Weber, 2004). In the Loxocarpinae only dry capsules are found. The most common shape is cylindrical, with longitudinal dehiscence into two valves (Fig. 1A-1B). Most twisted capsules have this structure, or, less frequently, are conical, as in the group of *Paraboea* species with a bilabiate calyx. Straight fruit types need to be further categorised. Most straight capsules, like the twisted ones, dehisce into two valves along two suture lines. The straight fruits of

Orchadocarpa and *Paraboea* (except for *P. incudicarpa* B.L.Burtt) have this morphology, and ortho- and plagiocarpic forms exist. A variation of this morphology is seen in *Loxocarpus*, where the short, conical and plagiocarpic capsule has two dorso-ventral valves which are strongly unequal and whose dehiscence results in a cup for splash dispersal (Fig. 1C). *Paraboea incudicarpa*, *Somrania* and *Emarhendia*, instead, produce capsules that are plagiocarpic and cylindrical but, unlike those of e.g. *Orchadocarpa*, dehisce only along the upper suture line (Fig. 1D).
While most genera of Loxocarpinae have exclusively twisted or straight fruits, few have both types represented among their species. Genera with an exclusively straight fruit are *Emarhendia*, *Loxocarpus*, *Orchadocarpa* and *Somrania,* although all with substantially different types of capsules. Genera with an exclusively twisted fruit are *Dorcoceras*, *Rhabdothamnopsis*, *Senyumia* and *Spelaeanthus*. Finally, genera where both states are present are *Boea*, *Damrongia*, *Kaisupeea*, *Middletonia*, *Ornithoboea* and *Paraboea*.

Despite the obvious difference in fruit morphologies, there does not appear to be any clear pattern across the phylogenetic trees. A lack of consistency was already inferred by Burtt (1984), when he modified the generic boundaries of *Boea* and *Paraboea* hitherto based on the fruit twisting. In our phylogeny, the position of *Middletonia* and *Dorcoceras* suggests that a twisted fruit is the ancestral condition, and that straight fruits have evolved several times in the Loxocarpinae. This mirrors the evolution of the other subtribe of Gesneriaceae with a predominantly twisted fruit, the Streptocarpinae, where multiple independent losses of fruit twist have been inferred by Nishii et al. (in press). In order to make further progress in our understanding of the evolution of the fruit in the Loxocarpinae, however, a more in-depth carpological study is necessary.

While the variation in fruit type does not form a clear pattern in the tree topology, distribution data show a geographic line along the Isthmus of Kra in Peninsular Thailand. This is most remarkable in *Paraboea*, where two subclades (with e.g. *P. crassifolia* (Hemsl.) B.L.Burtt and *P. acutifolia* (Ridl.) B.L.Burtt) comprise species predominantly from south and north of the Isthmus, respectively. Species of the two groups are not as distinct morphologically as they are geographically and genetically. The same situation is present in the third subclade of *Paraboea* (with e.g. *P. subplana* (B.L.Burtt) C.Puglisi), sister to the species found south of Kra, where the two main

branches show a well-supported separation between species found on either side of the Isthmus.

In *Ornithoboea*, conversely, the three species found south of the Isthmus of Kra are morphologically distinct from their northern congenerics (Scott & Middleton, 2014), although the current phylogeny does not provide unambiguous support for a matching genetic differentiation.

Emarhendia, *Orchadocarpa*, *Senyumia*, *Somrania*, *Spelaeanthus* and all the species currently placed in *Loxocarpus* are entirely restricted to south of the Isthmus of Kra. *Boea* is only present much further east. *Middletonia* and *Damrongia* have species both south and north of the Isthmus of Kra, but the relationships between the species are not yet sufficiently resolved to test whether there is a significant biogeographical element to them. Additionally, *Damrongia trisepala* has a distribution that straddles the Isthmus of Kra, a rare occurrence in the Loxocarpinae.

Dorcoceras has a different distribution pattern from the other Loxocarpinae. Most species occur on the Asian continent, and one species, *D. philippense*, is broadly distributed in China, Laos, Vietnam, the Philippines and central Indonesia. This might suggest a migration from the continent to Indonesia through the Philippines, which differs from the pattern observed in the rest of the tribe Trichosporeae (Weber, 2004; Cronk & al., 2005; Möller & al., 2009, 2011), involving migration from China southwards, along the Thai/Malay Peninsula and then west to east across Malesia. The different route of migration of *Dorcoceras* does not touch the Isthmus of Kra and neither seems to cross any other discontinuity line to the east or the west.

Taxonomic treatment

Boea Comm. ex Lam., Encycl. 1: 401. 1785 – Type: *Boea magellanica* Comm. ex Lam. Fig. 3: 3f.

Ten species, distributed in Eastern Indonesia, Papua New Guinea, the Solomon Islands and Queensland (Australia). This is the only genus of the Loxocarpinae to have an Australasian distribution. *Boea* has a flat-faced corolla, exserted stamens, a twisted, orthocarpic capsule and a thin, simple indumentum on the lower surface of the leaf.

Species list: *Boea dennisii* B.L.Burtt, *Boea hemsleyana* B.L.Burtt, *Boea hians* Burkill, *Boea hygroscopica* F.Muell., *Boea kinnearii* (F.Muell.) B.L.Burtt, *Boea lawesii* H.O.Forbes, *Boea magellanica* Comm. ex Lam., *Boea mollis* Schltr., *Boea rosselensis* B.L.Burtt, *Boea urvillei* C.B.Clarke.

Damrongia Kerr ex Craib in Bull. Misc. Inform. Kew 1918(10): 364. 1918 – Type: *Damrongia purpureolineata* Kerr ex Craib. Fig. 3: 6a-6c.

With the inclusion of *Boea clarkeana* and the three Asian species of *Streptocarpus*, and with the synonymisation of *Damrongia cyanantha* into *D. trisepala*, *Damrongia* is now a genus of ten species, centred in Thailand and distributed from China to Sumatra. All species have an infundibuliform-tubular corolla and a chiritoid stigma, and the species for which a count is available, all have chromosome number 2n=18 (Christie et al., 2012; Möller & Pullan, 2015 onwards). The new circumscription has broadened the range of morphological variation of *Damrongia*, with the addition of characters such as the caulescent habit and the twisted, orthocarpic fruit.

The following are the new combinations in *Damrongia*.

Damrongia burmanica (Craib) C.Puglisi, **comb. nov**. ≡ *Streptocarpus burmanicus* Craib in Notes Roy. Bot. Gard. Edinburgh 11(55): 253. 1919 – Lectotype (designated by Hilliard & Burtt, 1971: 370): Upper Burma, Meiktila district, Taunggyigon Reserve, *Mg Tha Myaing 262* (E barcode E00155311 (sheet 1) – E00155312 (sheet 2); isolectotype K, n.v.).

Damrongia clarkeana (Hemsl.) C.Puglisi, **comb. nov.** ≡ *Boea clarkeana* Hemsl. in J. Linn. Soc., Bot. 26(174): 232–233. 1890 ≡ *Dorcoceras clarkeanum* (Hemsl.) Schltr. in Bot. Jahrb. Syst. 58: 259. 1923 ≡ *Streptocarpus clarkeanus* (Hemsl.) Hilliard & B.L.Burtt, Streptocarpus: Afr. Pl. Study: 388. 1971 – Holotype: China, Hupeh (Hubei), Nanto and mountains to the northward and South Tunghu, *Henry 7584* (K barcode K000249894; isotypes NY barcode NY01287860, US barcode US00064695).

= *Boea mairei* H.Lév. in Repert. Spec. Nov. Regni Veg. 12(325–330): 286. 1913 – **Lectotype (designated here)**: China, Yunnan, rochers inaccessibles au soleil, pied des

montagnes a La-Kou, *Maire s.n.* (E barcode E00175310; isolectotype: G barcode G00303008).

= *Boea densihispidula* S.B.Zhou & X.H.Guo in Acta Phytotax. Sin. 29(5): 477–478, t.1. 1991 – Holotype: China, Anhui, Guichi, Tanxi, *Zhou Xiu-Fang 89053* (ANU n.v.; isotype: PE n.v.).

Damrongia orientalis (Craib) C.Puglisi, **comb. nov.** ≡ *Streptocarpus orientalis* Craib in Bull. Misc. Inform. Kew 1911(10): 432. 1911 – Lectotype (first step, designation of *Kerr 769* (K) by Hilliard & Burtt, 1971: 371, second step designated here): Thailand, Chiengmai [=Chiang Mai], Doi Sutep, *Kerr 769* (K barcode K000545610; isolectotypes: K barcode K000545611 and barcode K000545612, PH barcode PH00029114).

Damrongia sumatrana (B.L.Burtt) C.Puglisi, **comb. nov.** ≡ *Streptocarpus sumatranus* B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 24: 48. 1962 – Holotype: Indonesia, W. Sumatra, near Halaban, Pajakumbuh region, *Meijer 7560* (L barcode L0790314; isotype: SING barcode SING0194684).

Damrongia trisepala (Barnett) D.J.Middleton & A.Weber in Taxon 60(3): 778. 2011 ≡ *Chirita trisepala* Barnett in Nat. Hist. Bull. Siam Soc. 20: 18. 1961 – Lectotype (designated by Barnett, 1961: 255): Thailand, Chantaburi, Kao Sabap, *Put 905* (K barcode K000545608; isolectotypes: ABD, BK barcode BK257925, BKF n.v., BM barcode BM000997773).

= *Damrongia cyanantha* Triboun in Thai For. Bull., Bot. 38: 109. 2010, ***syn. nov.*** – Holotype: Thailand, Kamphaeng Phet, Khlong Lan Waterfall, *Triboun & Yothakaew 4289* (BK n.v.; isotypes: BKF n.v., E barcode E00576669).

Species list: *Damrongia burmanica* (Craib) C.Puglisi, *Damrongia clarkeana* (Hemsl.) C.Puglisi, *Damrongia cyanea* (Ridl.) D.J.Middleton & A.Weber, *Damrongia fulva* (Barnett) D.J.Middleton & A.Weber, *Damrongia integra* (Barnett) D.J.Middleton & A.Weber, *Damrongia lacunosa* (Hook. f.) D.J.Middleton & A.Weber, *Damrongia orientalis* (Craib) C.Puglisi, *Damrongia purpureolineata* Kerr ex Craib, *Damrongia*

sumatrana (B.L.Burtt) C.Puglisi, *Damrongia trisepala* (Barnett) D.J.Middleton & A.Weber.

Dorcoceras Bunge, Enum. Pl. Chin. Bor.: 54. 1832 (1833) **–** Type: *Dorcoceras hygrometricum* Bunge. Fig. 3: 2.

This genus is resurrected to accommodate the four species with a campanulate corolla excluded from *Boea*. *Dorcoceras* is found in China, Thailand, Cambodia, Vietnam, Philippines and Indonesia. *Dorcoceras* has a rosulate habit, simple indumentum, free calyx lobes and an obliquely campanulate, lilac corolla, with inserted stamens arising at the mouth. The new combinations needed are below.

Dorcoceras geoffrayi (Pellegr.) C.Puglisi, **comb. nov.** ≡ *Boea geoffrayi* Pellegr. in Bull. Soc. Bot. France 73: 425. 1926 **–** Lectotype (designated by Burtt, 1984: 420): Cambodia, Kampot, mont Pnom-Dong, *Geoffray 58* (P barcode P00606312).

Dorcoceras wallichii (R.Br.) C.Puglisi, **comb. nov.** ≡ *Boea wallichii* R.Br., On Cyrtandreae 124. 1839 ≡ *Didymocarpus helicteroides* Wall., Numer. List n. 789. 1829, *nom. nud*. **–** Type: Upper Burma, Toong Dong, *Wallich list n.789* (BM barcode BM000906643, K barcode K000249883).

Species list: *Dorcoceras geoffrayi* (Pellegr.) C.Puglisi, *Dorcoceras hygrometricum* Bunge, *Dorcoceras philippense* (C.B.Clarke) Schltr., *Dorcoceras wallichii* (R.Br.) C.Puglisi.

Emarhendia Kiew, A.Weber & B.L.Burtt in Beitr. Biol. Pflanzen 70(2–3): 398. 1997 (1998) **–** Type: *Emarhendia bettiana* (M.R.Hend) Kiew, A.Weber & B.L.Burtt (≡*Paraboea bettiana* M.R.Hend.). Fig. 3: 3b.

One species, endemic to Peninsular Malaysia, characterised by the plagiocarpic, straight fruit and the patch of glandular hairs between the two upper corolla lobes. Its relationships with *Loxocarpus* and *Orchadocarpa* are in need of further clarification.

Kaisupeea B.L.Burtt in Nordic J. Bot. 21(2): 115–119. 2001 – Type: *Kaisupeea herbacea* (C.B.Clarke) B.L.Burtt (≡ *Boea herbacea* C.B.Clarke). Fig. 3: 4a.

Three species from Burma and Thailand, characterised by the indumentum predominantly consisting of glandular hairs and the anthers hairy at the back. *Kaisupeea* is most closely related to *Rhabdothamnopsis*.

Species list: *Kaisupeea cyanea* B.L.Burtt, *Kaisupeea herbacea* (C.B.Clarke) B.L.Burtt, *Kaisupeea orthocarpa* B.L.Burtt.

Loxocarpus R.Br., Cyrtandreae: 120. 1839 – Type: *Loxocarpus incanus* R.Br. Fig. 3: 3a.

This recently revised genus (Yao, 2012) comprises 20−23 species, distributed in the Thai-Malay Peninsula, Sumatra and Borneo. Its most characteristic feature is the conical, plagiocarpic capsule, but it is otherwise highly variable in morphology. The phylogenetic analysis confirmed its non-monophyly and revealed the consistent presence of three distinct groups of species. Given the paucity of the material currently available for *Loxocarpus*, the genus is left untouched until further focused research, also involving the other Malaysian genera *Emarhendia* and *Orchadocarpa*.

Species list: *Loxocarpus angustifolius* Ridl., *Loxocarpus argenteus* B.L.Burtt, *Loxocarpus caeruleus* (Ridl.) Ridl., *Loxocarpus caulescens* B.L.Burtt, *Loxocarpus conicapsularis* (C.B.Clarke) B.L.Burtt, *Loxocarpus coodei* (B.L.Burtt) T.L.Yao, *Loxocarpus holttumii* M.R.Hend., *Loxocarpus incanus* R.Br., *Loxocarpus incanus* var. *sekayuensis* (Banka & Kiew) T.L.Yao, *Loxocarpus meijeri* B.L.Burtt, *Loxocarpus pauzii* T.L.Yao, *Loxocarpus repens* B.L.Burtt, *Loxocarpus rufescens* (C.B.Clarke) B.L.Burtt, *Loxocarpus semitortus* (C.B.Clarke) Ridl., *Loxocarpus sericeus* (Ridl.) B.L.Burtt, *Loxocarpus sericiflavus* (Banka & Kiew) T.L.Yao, *Loxocarpus stapfii* (Kraenzl.) B.L.Burtt, *Loxocarpus taeniophyllus* (B.L.Burtt) T.L.Yao, *Loxocarpus tunkui* Kiew, *Loxocarpus verbeniflos* (C.B.Clarke) B.L.Burtt, *Loxocarpus violoides* (C.B.Clarke) T.L.Yao.

Middletonia C.Puglisi, **gen. nov. –** Type: *Middletonia multiflora* (R.Br.) C.Puglisi. (≡ *Boea multiflora* R.Br.). Fig. 3: 1.

Similar to *Paraboea* (C.B.Clarke) Ridl. in having a matted indumentum on the abaxial side of the leaves but distinct by the farinose glandular indumentum on the ovary and the free and erect anthers.

= *Boea* sect. *Caulescentes* Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3B): 150. 1894 **–** Lectotype (designated by Burtt, 1954: 194): *Boea multiflora* R.Br.

Lithophytic, shortly caulescent, perennial herbs. Leaves opposite, those of a pair equal; lamina oblong to elliptic, apex obtuse to acute, base cuneate to obtuse, sometimes oblique, margin crenate or serrate, adaxial surface glabrescent, furfuraceous or pubescent, abaxial surface with a matted indumentum; veins raised beneath, more or less smooth above, tertiary veins reticulate and visible on the abaxial surface, especially in proximity to the leaf margin. Inflorescence an axillary cyme, many-flowered, densely tomentose; peduncles longer or shorter than the leaves; bracts inconspicuous. Calyx 5-merous, lobes divided to the base; lobes 1**–**3 mm long, narrowly ovate, glabrous or glandular inside, more or less tomentose outside. Corolla 5-merous, white, violet or blue, slightly bilabiate, 4**–**8(–10) mm long, 4**–**10 mm across, with or without an indumentum; tube 1–3 mm long; limb slightly 2-lipped, upper lip with 2 lobes 2–6(–9) × 1–6.5 mm, lower lip 3-lobed, lobes 2–6(–9) × 1–6.5 mm, all lobes spreading, flat. Stamens 2; filaments straight; anthers with a minute, glandular indumentum, not coherent, opening towards the top; staminodes 2, reduced or aborted. Ovary syncarpous, 2-carpellate, ovoid, with a farinose glandular indumentum, 1–2.5 × c. 1 mm, ovules many; style glabrous, 2.5–3 mm long; stigma capitate. Fruit a capsule, to 1.3 cm long, straight or twisted, retaining the indumentum of the ovary. Seeds minute, compressed.

Distribution: India, Bangladesh, Bhutan, China, Burma, Thailand, Laos, Cambodia, Vietnam, Malaysia.

Habitat: limestone or granite.

This new genus is segregated from *Paraboea* following the results of the phylogenetic study and the subsequent morphological investigation. The new combinations in *Middletonia* are given below.

Middletonia evrardii (Pellegr.) C.Puglisi, **comb. nov.** ≡ *Boea evrardii* Pellegr. in Lecomte, Fl. Indo-Chine 4: 550. 1930 ≡ *Paraboea evrardii* (Pellegr.) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 428. 1984 **–** Isolectotypes (designated by Burtt, 1984: 428): Vietnam, Lam Dong, Pongour near Di Linh, *Evrard 1177* (P barcode P00556499, P barcode P00622885).

= *Boea multiflora* var. *villosa* Pellegr. in Bull. Soc. Bot. France 73: 424. 1926. [pro parte] **–** Lectotype (designated by Xu & al., 2008: 276): Laos, Savannakhet, haut vours de la Tchépone a 500–600 m, dans les roches, *E. Poilane 12188* (P barcode P00634326).

Middletonia monticola (Triboun & D.J.Middleton) C.Puglisi, **comb. nov.** ≡ *Paraboea monticola* Triboun & D.J.Middleton in Gard. Bull. Singapore 64(2): 346. 2012 **–** Holotype: Thailand, Phangnga, Tai Toy, *Triboun 3662* (BK n.v.; isotype: E n.v.).

Middletonia multiflora (R.Br.) C.Puglisi, **comb. nov.** ≡ *Boea multiflora* R.Br., Pl. Jav. Rar. Cyrtandreae: 120. 1840 ≡ *Paraboea multiflora* (R.Br.) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 433. 1984 ≡ *Didymocarpus multiflorus* Wall., Numer. List. No.: 793. 1829, *nom. nud.* **–** Lectotype (designated by Xu & al., 2008: 276): Bangladesh, Pundua, Sylhet Mt., *De Silva in Wallich 793* (BM barcode BM000797995; isolectotype: K barcode K001111906).

= *Boea flocculosa* C.B.Clarke in Commelyn. Cyrtandr. Bengal. t. 83. 1874 **–** Lectotype (designated by Burtt, 1984: 434): India, Khasia Hills, *Hooker & Thomson s.n.* (K n.v.).

= *Boea multiflora* R.Br. var. *burmannica* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 144. 1883 **–** Lectotype (designated by Burtt, 1984: 434): Burma, Moulmein, *Parish 436* (K n.v.).

= *Boea microcarpa* Drake in Bull. Soc. Philom. Paris, ser. 8, 2: 130. 1890 ≡ *Paraboea microcarpa* (Drake) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 433. 1984 – Holotype: Vietnam, Quang Ninh, Tangkeuin, *Balansa 4302* (P barcode P00556510).

= *Boea thirionii* H.Lév. in Repert. Spec. Nov. Regni Veg. 11(286–290): 301. 1912 ≡ *Paraboea thirionii* (H.Lév.) B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 439. 1984 – Holotype: China, Kweichow, Gny-ken, *Esquirol 2699* (E barcode E00265058),

= *Boea multiflora* R.Br. var. *villosa* Pellegr. in Lecomte, Fl. Indo-Chine 4: 549. 1930 [pro parte] – Lectotype (designated by Xu & al., 2008: 276): Laos, Savannakhet, haut vours de la Tchépone a 500–600 m, dans les roches, *Poilane 12188* (P barcode P00634326).

= *Boea reticulata* Barnett, Nat. Hist. Bull. Siam Soc. 20: 20. 1961. Lectotype (designated by Barnett, 1961: 256): Thailand, Chiengmai, Me Wang, *Kerr 6356* (K barcode K000196614; isolectotype: ABD, BK barcode BK257920, BM barcode BM000906647).

Middletonia multiflora var. caulescens (Z.R.Xu & B.L.Burtt) C.Puglisi, **comb. nov.** ≡ *Paraboea multiflora* var. *caulescens* Z.R.Xu & B.L.Burtt in Edinburgh J. Bot. 48(1): 7–8. 1991 – Holotype: Thailand, Kanchanaburi, near Neekey, near Wangka, *G. Den Hoed Exp. No. 946* (L barcode L0003189).

Middletonia regularis (Ridl.) C.Puglisi, **comb. nov.** ≡ *Didymocarpus regularis* Ridl. J. Linn. Soc., Bot 32: 515. 1896 ≡ *Paraboea regularis* (Ridl.) Ridl. in J Straits Branch Roy. Asiat. Soc. 44: 68. 1905 – Lectotype (designated by Burtt, 1984: 435): *Curtis s.n.* (SING barcode SING0042998; isolectotype: E barcode E00451499).

Orchadocarpa Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 78. 1905 – Type: *Orchadocarpa lilacina* Ridl. Fig. 3: 3c.

Monotypic genus from Peninsular Malaysia. It is recognisable by the short fruit, completely enclosed by the calyx, and the flat-faced corolla with a lower lip longer than

620 the upper. The placement of *Orchadocarpa* in the phylogeny remains, like that of
621 *Emarhendia*, unresolved but likely to be somewhat close to part of *Loxocarpus*.

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624 **Ornithoboea** Parish ex C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 147. 1883
625 **–** Type: *Ornithoboea parishii* C.B.Clarke. Fig. 3: 4c.

626 This genus was revised recently (Scott & Middleton, 2014) and consists of 16 species
627 from China, Thailand, Burma, Vietnam, Laos and Malaysia. It is easily recognisable by
628 the palatal beard and the circlet of hairs around the corolla mouth. *Ornithoboea* was
629 found to be monophyletic and its closest relatives are *Rhabdothamnopsis* and
630 *Kaisupeea*.

631 Species list: *Ornithoboea arachnoidea* (Diels) Craib, *Ornithoboea barbanthera*
632 B.L.Burtt, *Ornithoboea calcicola* C.Y.Wu ex H.W.Li, *Ornithoboea emarginata*
633 D.J.Middleton & N.S.Lý, *Ornithoboea feddei* (H.Lév.) B.L.Burtt, *Ornithoboea flexuosa*
634 (Ridl.) B.L.Burtt, *Ornithoboea henryi* Craib, *Ornithoboea lacei* Craib, *Ornithoboea*
635 *maxwellii* S.M.Scott, *Ornithoboea multitorta* B.L.Burtt, *Ornithoboea obovata*
636 S.M.Scott, *Ornithoboea occulta* B.L.Burtt, *Ornithoboea parishii* C.B.Clarke,
637 *Ornithoboea pseudoflexuosa* B.L.Burtt, *Ornithoboea puglisiae* S.M.Scott, *Ornithoboea*
638 *wildeana* Craib.

639 **Paraboea** (C.B.Clarke) Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 63. 1905, *nom.*
640 *cons.* **–** Type: *Paraboea clarkei* B.L.Burtt. Fig. 3: 7.

641 The circumscription of *Paraboea*, recently modified by Puglisi & al. (2011a) is
642 modified again by the segregation of the new genus *Middletonia*. *Paraboea* now
643 consists of 127 species distributed throughout Southeast Asia. It is easily recognised by
644 the combination of a matted, interwoven indumentum on the lower side of the leaves,
645 the flat-faced to shortly campanulate corolla, the non-erect anthers and the lack of
646 sessile glands on the ovary.

Species list: *Paraboea acaulis* (Barnett) C.Puglisi, *Paraboea acuta* (C.B.Clarke) C.Puglisi, *Paraboea albida* (Barnett) C.Puglisi, *Paraboea amplexicaulis* (Parish ex C.B.Clarke) C.Puglisi, *Paraboea angustifolia* Yan Liu & W.B.Xu, *Paraboea arachnoidea* Triboun, *Paraboea axillaris* Triboun, *Paraboea bakeri* M.R.Hend., *Paraboea banyengiana* B.L.Burtt, *Paraboea barnettiae* C.Puglisi, *Paraboea berouwensis* Z.R.Xu & B.L.Burtt, *Paraboea bhumiboliana* Triboun & Chuchan, *Paraboea bintangensis* B.L.Burtt, *Paraboea birmanica* (Craib) C.Puglisi, *Paraboea brachycarpa* (Ridl.) B.L.Burtt, *Paraboea brunnescens* B.L.Burtt, *Paraboea burttii* Z.R.Xu, *Paraboea caerulescens* (Ridl.) B.L.Burtt, *Paraboea candidissima* B.L.Burtt, *Paraboea capitata* Ridl., *Paraboea capitata* var. *oblongifolia* Ridl., *Paraboea changjiangensis* F.W.Xing & Z.X.Li, *Paraboea chiangdaoensis* Z.R.Xu & B.L.Burtt, *Paraboea clarkei* B.L.Burtt, *Paraboea cochinchinensis* (C.B.Clarke) B.L.Burtt, *Paraboea crassifolia* (Hemsl.) B.L.Burtt, *Paraboea culminicola* K.G.Pearce, *Paraboea detergibilis* (C.B.Clarke) B.L.Burtt, *Paraboea dictyoneura* (Hance) B.L.Burtt, *Paraboea divaricata* (Ridl.) B.L.Burtt, *Paraboea doitungensis* Triboun & D.J.Middleton, *Paraboea eburnea* Triboun, *Paraboea effusa* B.L.Burtt, *Paraboea elegans* (Ridl.) B.L.Burtt, *Paraboea ferruginea* (Ridl.) Ridl., *Paraboea filipes* (Hance) B.L.Burtt, *Paraboea glabra* (Ridl.) B.L.Burtt, *Paraboea glabrescens* (Barnett) C.Puglisi, *Paraboea glabriflora* (Barnett) B.L.Burtt, *Paraboea glabrisepala* B.L.Burtt, *Paraboea glandulifera* (Barnett) C.Puglisi, *Paraboea glanduliflora* Barnett, *Paraboea glandulosa* (B.L.Burtt) C.Puglisi, *Paraboea glutinosa* (Hand.-Mazz.) K.Y.Pan, *Paraboea gracillima* Kiew, *Paraboea graniticola* Z.R.Xu, *Paraboea guilinensis* L.Xu & Y.G.Wei, *Paraboea hainanensis* (Chun) B.L.Burtt, *Paraboea halongensis* Kiew & T.H.Nguyên, *Paraboea harroviana* (Craib) Z.R.Xu, *Paraboea harroviana* var. *ovata* Z.R.Xu, *Paraboea havilandii* (Ridl.) B.L.Burtt, *Paraboea hekouensis* Y.M. Shui & W.H. Chen, *Paraboea incudicarpa* B.L.Burtt, *Paraboea insularis* Triboun, *Paraboea kalimantanensis* Z.R.Xu & B.L.Burtt, *Paraboea lambokensis* Kiew, *Paraboea lanata* (Ridl.) B.L.Burtt, *Paraboea lancifolia* (Ridl.) B.L.Burtt, *Paraboea lavandulodora* Triboun, *Paraboea laxa* Ridl., *Paraboea leopoldii* K.M.Wong, J.T.Pereira, Sugau & S.P.Lim, *Paraboea leporina* (H.J.Lam) B.L.Burtt, *Paraboea leuserensis* B.L.Burtt, *Paraboea longipetiolata* (B.L.Burtt) C.Puglisi, *Paraboea luzoniensis* Merr., *Paraboea maculata* C.Puglisi, *Paraboea mahaxayana* Z.R.Xu & B.L.Burtt, *Paraboea*

679 *manhaoensis* Y.M. Shui & W.H. Chen, *Paraboea martinii* (H.Lév.) B.L.Burtt,
680 *Paraboea mataensis* Z.R.Xu & B.L.Burtt, *Paraboea meiophylla* B.L.Burtt, *Paraboea*
681 *middletonii* Triboun, *Paraboea minahassae* (Teijsm. & Binn.) B.L.Burtt, *Paraboea*
682 *minor* (Barnett) B.L.Burtt, *Paraboea minuta* (Kraenzl.) B.L.Burtt, *Paraboea nana*
683 Triboun & Dongkumfu, *Paraboea nervosissima* Z.R.Xu & B.L.Burtt, *Paraboea*
684 *neurophylla* (Collett & Hemsl.) B.L.Burtt, *Paraboea nobilis* Triboun & D.J. Middleton,
685 *Paraboea nutans* D.Fang & D.H.Qin, *Paraboea obovata* Ridl., *Paraboea obtusa*
686 (C.B.Clarke) C.Puglisi, *Paraboea paniculata* (Ridl.) B.L.Burtt, *Paraboea paramartinii*
687 Z.R.Xu & B.L.Burtt, *Paraboea paraprimuloides* Z.R.Xu, *Paraboea parviflora* (Ridl.)
688 B.L.Burtt, *Paraboea patens* (Ridl.) B.L.Burtt, *Paraboea peltifolia* D.Fang & L.Zeng,
689 *Paraboea peninsularis* Triboun & D.J. Middleton, *Paraboea phanomensis* Triboun &
690 D.J. Middleton, *Paraboea prazeri* (B.L.Burtt) C.Puglisi, *Paraboea primuloides* Z.R.Xu,
691 *Paraboea prolixa* (C.B.Clarke) B.L.Burtt, *Paraboea pubicorolla* Z.R.Xu & B.L.Burtt,
692 *Paraboea punggulensis* Kiew, *Paraboea quercifolia* Triboun, *Paraboea rabilii* Z.R.Xu
693 & B.L.Burtt, *Paraboea robusta* (B.L.Burtt) C.Puglisi, *Paraboea rosea* Triboun,
694 *Paraboea rufescens* (Franch.) B.L.Burtt, *Paraboea rufescens* var. *tomentosa* (Barnett)
695 Z.R.Xu, *Paraboea sabahensis* Z.R.Xu & B.L.Burtt, *Paraboea sangwaniae* Triboun,
696 *Paraboea scabriflora* B.L.Burtt, *Paraboea schefferi* (H.O.Forbes) B.L.Burtt, *Paraboea*
697 *schefferi* var. *ambigua* (C.B.Clarke) Z.R.Xu, *Paraboea siamensis* Triboun, *Paraboea*
698 *sinensis* (Oliv.) B.L.Burtt, *Paraboea speciosa* (Rech.) B.L.Burtt, *Paraboea*
699 *speluncarum* (B.L.Burtt) B.L.Burtt, *Paraboea strobilacea* (Barnett) C.Puglisi,
700 *Paraboea subplana* (B.L.Burtt) C.Puglisi, *Paraboea suffruticosa* (Ridl.) B.L.Burtt,
701 *Paraboea swinhoei* (Hance) B.L.Burtt, *Paraboea takensis* Triboun, *Paraboea*
702 *tarutaoensis* Z.R.Xu & B.L.Burtt, *Paraboea tenuicalyx* Triboun, *Paraboea*
703 *tetrabracteata* F.Wen, Xin Hong & Y.G.Wei, *Paraboea thorelii* (Pellegr.) B.L.Burtt,
704 *Paraboea trachyphylla* Z.R.Xu & B.L.Burtt, *Paraboea treubii* (H.O.Forbes) B.L.Burtt,
705 *Paraboea trisepala* W.H.Chen & Y.M.Shui, *Paraboea umbellata* (Drake) B.L.Burtt,
706 *Paraboea uniflora* Z.R.Xu & B.L.Burtt, *Paraboea vachareea* Triboun & Sonsupab,
707 *Paraboea variopila* Z.R.Xu & B.L.Burtt, *Paraboea velutina* (W.T.Wang & C.Z.Gao)
708 B.L.Burtt, *Paraboea verticillata* (Ridl.) B.L.Burtt, *Paraboea vulpina* Ridl., *Paraboea*
709 *xylocaulis* Triboun.

Rhabdothamnopsis Hemsl. in J. Linn. Soc., Bot. 35(247): 517–518. 1903 – Type: *Rhabothamnopsis sinensis* Hemsl. Fig. 3: 4b.

Monotypic genus from China whose closest relative is *Kaisupeea*. It is characterised by the solitary flowers with infundibuliform corollas and the twisted fruit.

Senyumia Kiew, A.Weber & B.L.Burtt in Beitr. Biol. Pflanzen 70(2–3): 400. 1997. (1998) – Type: *Senyumia minutiflora* (Ridl.) Kiew, A.Weber & B.L.Burtt ≡ *Boea minutiflora* Ridl. Fig. 3: 3d.

This is another monotypic genus from Peninsular Malaysia. Its closest relatives are *Boea* and *Spelaeanthus*. It is the only twisted-fruited genus to have a resupinate flower.

Somrania D.J.Middleton in Thai For. Bull. (Bot.) 40: 10. 2012 – Type: *Somrania albiflora* D.J.Middleton. Fig. 3: 5.

Somrania is closely related to *Damrongia* and consists of three species endemic to southern Thailand. The genus is easily recognisable by its tubular corolla and the indumentum of branched hairs.

Species list: *Somrania albiflora* D.J.Middleton, *Somrania flavida* D.J.Middleton & Triboun, *Somrania lineata* D.J.Middleton & Triboun.

Spelaeanthus Kiew, A.Weber & B.L.Burtt in Beitr. Biol. Pflanzen 70(2–3): 401. 1997. (1998) – Type: *Spelaeanthus chinii* Kiew, A.Weber & B.L.Burtt. Fig. 3: 3e.

One species from Peninsular Malaysia, closely related to *Senyumia* and *Boea*. *Spelaeanthus* has a characteristic white, bowl-shaped corolla.

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875

876 **Tables**

877 Table 1: The '2-markers' dataset comprises ITS and *trnL-trnF* sequences; the '3-
878 markers' dataset comprises ITS, *trnL-trnF* and *ndhF-trnL*^{UAG} sequences.

Dataset	Taxa ingroup	Taxa outgroup	Total characters	Included characters	PICs
2-markers	136	6	2271	1913	677
3-markers	64	4	4499	3997	1013

879

880

881 Table 2: Statistical support for the main clades identified. Values are shown as
882 'bootstrap/posterior probability'.

883

Clade	2-markers	3-markers
Ingroup	85/1	98/1
Clade 1 (*Middletonia*)	100/1	100/1

Clade 2 (*Dorcoceras*)	100/1	100/1
Clade 3 (*Loxocarpus*/*Orchadocarpa*/*Emarhendia*/*Senyumia*/*Spelaeanthus*/*Boea*)	-/0.64	-/1
Clade 4 (*Ornithoboea*/*Kaisupeea*/*Rhabdothamnopsis*)	59/1	88/1
Clade 5 (*Somrania*)	100/1	100/1
Clade 6 (*Damrongia*)	91/1	100/1
Clade 7 (*Paraboea*)	95/1	100/1

884

885 **Figure captions**

886 Figure 1: Capsule diversity in the Loxocarpinae. A: straight capsule with two
887 longitudinal dehiscence lines. *Paraboea burttii* Z.R.Xu. B: twisted capsule with two
888 longitudinal dehiscence lines. *Ornithoboea puglisiae* S.M.Scott. C: splash cup with
889 dorso-ventral dehiscence. *Loxocarpus incanus* R.Br.. D: straight capsule dehiscing only
890 along the upper suture. *Paraboea incudicarpa* B.L.Burtt. Photo credits: D. Middleton
891 (A, D), P. Karaket (B) and T. Phutthai (C)

892 Figure 2: Phylogeny of the Loxocarpinae. The overall structure of the subtribe is
893 represented by this 50% majority rule consensus tree derived from the Bayesian
894 analysis of the dataset available for the three markers ITS, *trnL-trnF* and *ndhF-trn*^{LUAG}.
895 The numbers in bold font inside circles refer to the clade numbering used in the text.
896 The numbers by the nodes are the posterior probabilities, followed by the bootstrap
897 values returned by the Parsimony analysis of the same dataset. The bars at the right of
898 the tree mark the placement of the recircumscribed genera. Asterisks mark accessions of
899 the type species.

900 Figure 3: The seven clades of Loxocarpinae. 1: *Middletonia* C.Puglisi, a new genus
901 including the species with a farinose indumentum on the ovary, segregated from
902 *Paraboea* (C.B.Clarke) Ridl.. *Middletonia multifora* (R.Br.) C.Puglisi. Photos by D.
903 Middleton. 2: *Dorcoceras* Bunge is resurrected to include the Southeast Asian species
904 with a campanulate corolla previously ascribed to *Boea*. Left: *Dorcoceras* sp. nov.;

right: *D. philippense* (C.B.Clarke) Schltr.. Photos by P. Karaket. 3: clade dominated by a paraphyletic *Loxocarpus*, including the small Malesian genera. 3a: *Loxocarpus incanus* R.Br.. Photo by T. Putthai. 3b: *Emarhendia bettiana* (M.R.Hend) Kiew, A.Weber & B.L.Burtt. Photo by J. Tan. 3c: *Orchadocarpa lilacina* Ridl.. Photo by T.L. Yao. 3d: *Senyumia minutiflora* (Ridl.) Kiew, A.Weber & B.L.Burtt. Photo by P.T. Ong. 3e: *Spelaeanthus chinii* Kiew, A.Weber & B.L.Burtt. Photo by P.T. Ong. 3f: *Boea hygroscopica* F.Muell.. Photo by D. Middleton. 4: clade of three well-defined genera, left unaltered by this study. 4a: *Kaisupeea herbacea* (C.B.Clarke) B.L.Burtt. Photo by P. Triboun. 4b: *Rhabothamnopsis sinensis* Hemsl.. Photo by M. Möller. 4c: *Ornithoboea pseudoflexuosa* B.L.Burtt. Photo by P. Karaket. 5: *Somrania* D.J.Middleton, a small Thai genus, sister to *Damrongia* Kerr ex Craib. *Somrania flavida* D.J.Middleton & Triboun. Photo by D. Middleton. 6: *Damrongia*, expanded to include *Boea clarkeana* Hemsl. and the Asian species of *Streptocarpus* Lindl.. 6a: *Damrongia orientalis* (Craib) C.Puglisi. Photo by D. Middleton. 6b: *Damrongia trisepala* (Barnett) D.J.Middleton & A.Weber. Photo by P. Triboun. 6c: *Damrongia clarkeana* (Hemsl.) C.Puglisi. Photo by C. Puglisi. 7: *Paraboea*, recircumscribed in this study by the segregation of *Middletonia*. *Paraboea middletonii* Triboun. Photo by P. Karaket.

Electronic supplements

S1: Strict consensus of the six most parsimonious trees based on Parsimony analysis of the 2-markers dataset, including ITS and *trnL-trnF* sequences. Tree length=4049, CI=0.3779, HI=0.6221, RI=0.7310. The numbers inside the circles refer to the clades as treated in the text. The numbers above the branches represent bootstrap values. The bars at the right of the tree mark the placement of the recircumscribed genera. Asterisks mark accessions of the type species.

S2: 50% majority rule consensus tree based on Bayesian Inference of the 2-markers dataset, including ITS and *trnL-trnF* sequences. Number of generations: 10 mln, sample frequency: 1000, burn-in: 2000, average standard deviation: 0.002797. The numbers beside nodes represent posterior probabilities. The scalebar represents the number of substitutions per site. The numbers inside the circles refer to the clades as treated in the text. The bars at the right of the tree mark the placement of the recircumscribed genera.

936 Asterisks mark accessions of the type species.

937 S3: Strict consensus of the eight most parsimonious trees based on Parsimony analysis
938 of the 3-markers dataset, including ITS, *trnL-trnF* and *ndhF-trnL*^{UAG} sequences. Tree
939 length=4271, CI=0.5273, HI=0.4727, RI=0.6824. The numbers inside the circles refer
940 to the clades as treated in the text. The numbers above the branches represent bootstrap
941 values. The bars at the right of the tree mark the placement of the recircumscribed
942 genera. Asterisks mark accessions of the type species.

943 S4: 50% majority rule consensus tree based on Bayesian Inference of the 3-markers
944 dataset, including ITS, *trnL-trnF* and *ndhF-trnL*^{UAG} sequences. Number of generations:
945 10 mln, sample frequency: 1000, burn-in: 2000, average standard deviation: 0.001572.
946 The numbers beside nodes represent posterior probabilities. The scalebar represents the
947 number of substitutions per site. The numbers inside the circles refer to the clades as
948 treated in the text. The bars at the right of the tree mark the placement of the
949 recircumscribed genera. Asterisks mark accessions of the type species.

950 **Appendix**

951 **Appendix 1:** Accessions used in the phylogenetic study. Entries are in the format
952 '**voucher name**, updated taxon name, collection locality, collection date, *collector,*
953 *number*, (herbarium). ITS Genbank accession, *trnL-trnF* Genbank accession, *ndhF-*
954 *trnL*^{UAG} Genbank accession'. The asterisks indicate sequences newly submitted to
955 Genbank.

956 **Boea clarkeana 1,** *Damrongia clarkeana* (Hemsl.) C.Puglisi, China, Jiangxi, Tian Mu
957 Shan, 1 vii 2008, *H.F. Lu, JBS II-2*. ITS: *KU203805; *trnL-trnF*: *KU203900; *ndhF-*
958 *trnL*^{UAG}: *KU203995. **Boea clarkeana 2,** *Damrongia clarkeana* (Hemsl.) C.Puglisi,
959 China, Shaanxi, Mian Xian, 4 viii 2010, *P. Zhou & M. Möller, ZP 2010-019A*, (E). ITS:
960 *KU203806; *trnL-trnF*: *KU203901; *ndhF-trnL*^{UAG}: *KU203996. **Boea geoffrayi,**
961 *Dorcoceras geoffrayi* (Pellegr.) C.Puglisi, Thailand, Si Sa Ket, Kantharalak, 26 viii
962 2012, *D.J. Middleton & al., 5658*, (E, BK, BKF). ITS: *KU203781; *trnL-trnF*:
963 *KU203876; *ndhF-trnL*^{UAG}: *KU203977. **Boea hygrometrica 1,** *Dorcoceras*
964 *hygrometricum* Bunge, China, Zhejiang, Jinhua, 16 vii 2009, *M. Möller & J.B. Chen,*
965 *MMO 09-1436*, (E). ITS: *KU203783; *trnL-trnF*: *KU203878; *ndhF-trnL*^{UAG}:

*KU203978. **Boea hygrometrica 2,** *Dorcoceras hygrometricum* Bunge, China, Shaanxi, Liu Ba, 31 viii 2005, ex cult. RBGE 20080104A, *M. Möller & L.M. Gao, MMO 05-687*, (E). ITS: *KU203782; *trnL-trnF*: *KU203877; *ndhF-trnL*^{UAG}: *KU203979. **Boea hygrometrica 3,** *Dorcoceras hygrometricum* Bunge, China, Shaanxi, Liu Ba, 31 viii 2005, *M. Möller & L.M. Gao, MMO 05-686*, (E). ITS: *KU203784; *trnL-trnF*: *KU203879. **Boea hygroscopica 1,** *Boea hygroscopica* F.Muell., Australia, Queensland, Tchupala Falls, 11 vii 1994, ex cult. RBGE 19970386, *B. Tan & al., 443*, (E). ITS: FJ501320; *trnL-trnF*: *KU203903; *ndhF-trnL*^{UAG}: *KU204000. **Boea hygroscopica 2,** *Boea hygroscopica* F.Muell., Australia, Queensland, Palmerston NP, *A. Weber, 810808-1/1*, (WU). ITS: xxxxxxxx*; trnL-trnF*: FJ501477. **Boea lawesii,** *Boea lawesii* H.O.Forbes, Papua New Guinea, Morobe, Mumeng, 16 iv 1987, *Lambinon, 87/380*, (L), formerly identified as *B. magellanica*. ITS: FJ501321; *trnL-trnF*: FJ501478. **Boea philippensis 1,** *Dorcoceras philippense* (C.B.Clarke) Schltr., China, Guangxi, Tian Ling, 27 viii 2006, *M. Möller & Y.G. Wei, MMO 06-814*, (E). ITS: *KU203785; *trnL-trnF*: *KU203880; *ndhF-trnL*^{UAG}: *KU203980. **Boea philippensis 2,** *Dorcoceras philippense* (C.B.Clarke) Schltr., China, Yunnan, Huize, 23 vii 2010, *M. Möller & P. Zhou, MMO 10-1672A*, (E). ITS: *KU203786; *trnL-trnF*: *KU203881. **Boea philippensis 3,** *Dorcoceras philippense* (C.B.Clarke) Schltr., China, Hainan, Chang Jiang, 13 vii 2007, ex cult. RBGE 20080217, *M. Möller & Y.G. Wei MMO 07-1156*, (E). ITS: *KU203787; *trnL-trnF*: *KU203882. **Boea philippensis 4,** *Dorcoceras philippense* (C.B.Clarke) Schltr., Indonesia, Sulawesi, Gunung Ali, 28 iv 2002, ex cult. RBGE 20021242, *S.M. Scott, Scott 02-142*, (E). ITS: *KU203788; *trnL-trnF*: *KU203883; *ndhF-trnL*^{UAG}: *KU203981. **Boea sp.,** *Boea* sp., Papua New Guinea, Madang, 19 viii 1955, *Hoogland, 5129*, (CANB). ITS: *KU203809; *trnL-trnF*: * KU203904. **Boea sp.nov.,** *Dorcoceras* sp. nov., Thailand, Kanchanaburi, Sai Yok, 7 viii 2012, *D.J. Middleton & al., 5283*, (E, BK, BKF). ITS: *KU203780; *trnL-trnF*: *KU203875; *ndhF-trnL*^{UAG}: *KU203976. **Codonoboea elata,** *Codonoboea elata* (Ridl.) Rafidah, Malaysia, Perak, Maxwell Hill, *A.R. Rafidah, FRI 64321*, (KEP). ITS: JF912550; *trnL-trnF*: JF912523. **Codonoboea leucocodon,** *Codonoboea leucocodon* (Ridl.) Ridl., Malaysia, Pahang, Gunung Tahan, *C.L. Lim*, *s.n.,* (KEP). ITS: *KU203779; *trnL-trnF*: *KU203873. **Damrongia cyanantha,** *Damrongia trisepala* (Barnett) D.J.Middleton & A.Weber, Thailand,

Khampaeng Phet, Namtok Khlang An, *P. Triboun, s.n. (EDNA09_02232)*, (BK). ITS: *KU203802; *trnL-trnF*: *KU203897. **Damrongia fulva,** *Damrongia fulva* (Barnett) D.J.Middleton & A.Weber, Thailand, Nakhon Si Thammarat, Thung Song, 11 ix 2010, *D.J. Middleton & al., 5393*, (E). ITS: *KU203799; *trnL-trnF*: *KU203894; *ndhF-trnL*^{UAG}: *KU203993. **Damrongia lacunosa 1,** *Damrongia lacunosa* (Hook. f.) D.J.Middleton & A.Weber, Malaysia, Pahang, *A. Weber, 870510-1/8*, (WU). ITS: FJ501308; *trnL-trnF*: FJ501458. **Damrongia lacunosa 2,** *Damrongia lacunosa* (Hook. f.) D.J.Middleton & A.Weber, Malaysia, *Imin & al., FRI 63238*, (KEP). ITS: *KU203801; *trnL-trnF*: *KU203896; *ndhF-trnL*^{UAG}: *KU203991. **Damrongia purpureolineata 1***, Damrongia purpureolineata* Kerr ex Craib, Thailand, Lamphun, Li, 9 ix 2009, *D.J. Middleton & al., 4812*, (BK, BKF, E). ITS: JF912562; *trnL-trnF*: JF912535. **Damrongia purpureolineata 2,** *Damrongia purpureolineata* Kerr ex Craib, Thailand, Lamphun, Li, *P. Triboun, s.n. (CH111)*, (BK). ITS: *KU203798; *trnL-trnF*: *KU203893. **Damrongia trisepala 1,** *Damrongia trisepala* (Barnett) D.J.Middleton & A.Weber, Thailand, Chanthaburi, Khao Khitchakut, 27 viii 2012, *D.J. Middleton & al., 5676*, (BK, BKF, E). ITS: *KU203803; *trnL-trnF*: *KU203898; *ndhF-trnL*^{UAG}: *KU203994. **Damrongia trisepala 2,** *Damrongia trisepala* (Barnett) D.J.Middleton & A.Weber, Thailand, Prachin Buri, Na Di, 20 viii 2012, *D.J. Middleton & al., 5626*, (BK, BKF, E). ITS: *KU203804; *trnL-trnF*: *KU203899. **Didissandra elongata ssp. minor,** *Didissandra elongata* (Jack) C.B.Clarke subsp. *minor* (Ridl.) A.Weber & B.L.Burtt, Indonesia, Sumatra, Bengkulu, 1 vii 2011, *C. Puglisi & al., CP186*, (BO, E). ITS: KP325420; *trnL-trnF*: KP325427; *ndhF-trnL*^{UAG}: *KU203975. **Didissandra sp.,** *Didissandra* sp., Indonesia, Sumatra, West Sumatra, 24 vi 2011, *C. Puglisi & al., CP130*, (BO, E). ITS: KP325422; *trnL-trnF*: KP325429; *ndhF-trnL*^{UAG}: *KU203974. **Emarhendia bettiana,** *Emarhendia bettiana* (M.R.Hend) Kiew, A.Weber & B.L.Burtt, Malaysia, Pahang, *R. Kiew & al., 55716*, (KEP). ITS: HQ632955; *trnL-trnF*: HQ632864; *ndhF-trnL*^{UAG}: *KU203997. **Kaisupeea cyanea,** *Kaisupeea cyanea* B.L.Burtt, Thailand, Chachoengsao, 6 xi 1993, ex cult. RBGE 19972918, *K. Larsen 44272*, (E), formerly identified as *K. herbacea*. ITS: FJ501309; *trnL-trnF*: FJ501459. **Kaisupeea herbacea 1**, *Kaisupeea herbacea* (C.B.Clarke) B.L.Burtt, Thailand, Chiang Mai, Chom Tong, 19 ix 2008, *D.J. Middleton & al., 4518*, (E). ITS: *KU203830; *trnL-trnF*: *KU203925; *ndhF-trnL*^{UAG}: *KU204001. **Kaisupeea herbacea 2,** *Kaisupeea*

herbacea (C.B.Clarke) B.L.Burtt, Thailand, Prachin Buri, Na Di, 20 viii 2012, *D.J. Middleton & al., 5625*, (BK, BKF, E). ITS: *KU203832; *trnL-trnF*: *KU203927. **Kaisupeea herbacea 3,** *Kaisupeea herbacea* (C.B.Clarke) B.L.Burtt, Thailand, Kanchanaburi, Sai Yok, 7 viii 2012, *D.J. Middleton & al., 5282*, (BK, BKF, E). ITS: *KU203831; *trnL-trnF*: *KU203926. **Kaisupeea orthocarpa 1,** *Kaisupeea orthocarpa* B.L.Burtt, Thailand, Surat Thani, 27 ii 2006, ex cult. RBGE 20060623, *D.J. Middleton, 4200*, (E). ITS: *KU203834; *trnL-trnF*: *KU203929. **Kaisupeea orthocarpa 2,** *Kaisupeea orthocarpa* B.L.Burtt, Thailand, Surat Thani, Phanom , 7 ix 2008, *D.J. Middleton & al., 4356*, (BKF, E). ITS: *KU203833; *trnL-trnF*: *KU203928; *ndhF-trnL*^{UAG}: *KU204002. **Loxocarpus angustifolius 1,** *Loxocarpus angustifolius* Ridl., Malaysia, *FRIM staff, FRI 56313*, (KEP). ITS: *KU203824; *trnL-trnF*: *KU203919. **Loxocarpus angustifolius 2,** *Loxocarpus angustifolius* Ridl., Malaysia, Pahang, Gunung Tahan, *T.L. Yao, FRI 65288*, (KEP). ITS: *KU203825; *trnL-trnF*: *KU203920. **Loxocarpus_argenteus,** *Loxocarpus argenteus* B.L.Burtt, Malaysia, Sarawak, Bako NP, *T.L. Yao, FRI 57975*, (KEP). ITS: *KU203817; *trnL-trnF*: *KU203912; *ndhF-trnL*^{UAG}: *KU203985. **Loxocarpus holttumii 1,** *Loxocarpus holttumii* M.R.Hend., Malaysia, Johor, Gunung Panti, *T.L. Yao, FRI 65377*, (KEP). ITS: *KU203821; *trnL-trnF*: *KU203916; *ndhF-trnL*^{UAG}: *KU204012. **Loxocarpus holttumii 2,** *Loxocarpus holttumii* M.R.Hend., Malaysia, Malaya, *A. Weber, 840723-1/2*, (WU). ITS: HQ632956; *trnL-trnF*: FJ501479. **Loxocarpus incanus 1,** *Loxocarpus incanus* R.Br., Malaysia, Penang Hill, *T.L. Yao, KBG 2009-1300*, (KEP). ITS: *KU203814; *trnL-trnF*: *KU203909. **Loxocarpus incanus 2,** *Loxocarpus incanus* R.Br., Malaysia, Negeri Sembilan, Ulu Bendul, *T.L. Yao, FRI 65362*, (KEP). ITS: *KU203815; *trnL-trnF*: *KU203910; *ndhF-trnL*^{UAG}: *KU204013. **Loxocarpus incanus 3,** *Loxocarpus incanus* R.Br., Malaysia, Perak, Lata Puteh, *T.L. Yao, FRI 65394*, (KEP). ITS: *KU203816; *trnL-trnF*: *KU203911. **Loxocarpus incanus 4,** *Loxocarpus incanus* R.Br., Malaysia, *D.J. Middleton, 4379*, (E). ITS: *KU203810; *trnL-trnF*: *KU203905. **Loxocarpus incanus 5,** *Loxocarpus incanus* R.Br., Thailand, Nakhon Si Thammarat, 23 ix 2010, *D.J. Middleton & al., 5517*, (BK, BKF, E). ITS: *KU203811; *trnL-trnF*: *KU203906. **Loxocarpus incanus var. sekayuensis 1,** *Loxocarpus incanus* var. *sekayuensis* (Banka & Kiew) T.L.Yao, Malaysia, Terengganu, Gunung Tebu, *T.L. Yao, FRI 65450*, (KEP). ITS: *KU203813; *trnL-trnF*: *KU203908.

Loxocarpus incanus var. sekayuensis 2, *Loxocarpus incanus* var. *sekayuensis* (Banka & Kiew) T.L.Yao, Malaysia, Terengganu, Lata Sekayu Recreational Forest, *T.L. Yao, FRI 65445*, (KEP). ITS: *KU203812; *trnL-trnF*: *KU203907; *ndhF-trnL*^{UAG}: *KU204014. **Loxocarpus repens,** *Loxocarpus repens* B.L.Burtt, Malaysia, Sabah, Crocker Range Park, *T.L. Yao, FRI 65457*, (KEP). ITS: *KU203820; *trnL-trnF*: *KU203915. **Loxocarpus rufescens,** *Loxocarpus rufescens* (C.B.Clarke) B.L.Burtt, Malaysia, Sarawak, Gunung Santubong, *T.L. Yao, FRI 57968*, (KEP). ITS: *KU203822; *trnL-trnF*: *KU203917; *ndhF-trnL*^{UAG}: *KU204011. **Loxocarpus semitortus,** *Loxocarpus semitortus* (C.B.Clarke) Ridl., Malaysia, Johor, Gunung Ledang, *T.L. Yao, FRI 67914*, (KEP). ITS: *KU203823; *trnL-trnF*: *KU203918. **Loxocarpus sericiflavus 1,** *Loxocarpus sericiflavus* (Banka & Kiew) T.L.Yao, Malaysia, Johor, Sungai Yong, *T.L. Yao, FRI 57986*, (KEP). ITS: *KU203826; *trnL-trnF*: *KU203921; *ndhF-trnL*^{UAG}: *KU204010. **Loxocarpus sericiflavus 2,** *Loxocarpus sericiflavus* (Banka & Kiew) T.L.Yao, Malaysia, Johor, Gunung Belumut, *T.L. Yao, FRI 57999*, (KEP). ITS: *KU203827; *trnL-trnF*: *KU203922. **Loxocarpus verbeniflos,** *Loxocarpus verbeniflos* (C.B.Clarke) B.L.Burtt, Malaysia, Sabah, Tavui Forest Reserve, *T.L. Yao, FRI 65454*, (KEP). ITS: *KU203818; *trnL-trnF*: *KU203913. **Loxocarpus violoides,** *Loxocarpus violoides* (C.B.Clarke) T.L.Yao, Malaysia, Sabah, Kinabalu Park, *T.L. Yao, FRI 65458*, (KEP). ITS: *KU203819; *trnL-trnF*: *KU203914; *ndhF-trnL*^{UAG}: *KU203986. **Orchadocarpa lilacina,** *Orchadocarpa lilacina* Ridl, Malaysia, Pahang, *R. Kiew, 5410*, (KEP). ITS: HQ632954; *trnL-trnF*: HQ632863; *ndhF-trnL*^{UAG}: *KU204009. **Ornithoboea arachnoidea,** *Ornithoboea arachnoidea* (Diels) Craib, Thailand, Chiang Mai, Chiang Dao, 20 ix 2008, *D.J. Middleton & al., 4538*, (BK, BKF, E). ITS: JN934709; *trnL-trnF*: JN934751; *ndhF-trnL*^{UAG}: *KU204003. **Ornithoboea barbanthera,** *Ornithoboea barbanthera* B.L.Burtt, Thailand, Prachuap Khiri Khan, *D.J. Middleton & al., 4257*, (E). ITS: *KU203839; *trnL-trnF*: *KU203934; *ndhF-trnL*^{UAG}: *KU204004. **Ornithoboea flexuosa,** *Ornithoboea flexuosa* (Ridl.) B.L.Burtt, Malaysia, Kedah, Gunung Keriang, *A.R. Rafidah, FRI 64358*, (KEP). ITS: *KU203836; *trnL-trnF*: *KU203931; *ndhF-trnL*^{UAG}: *KU204005. **Ornithoboea maxwellii,** *Ornithoboea maxwellii* S.M.Scott, Thailand, Chiang Mai, Ban Pong, 6 vi 2004, *M. Möller & J.F. Maxwell, MMO 04-439*, (E). ITS: FJ501311; *trnL-trnF*: FJ501460. **Ornithoboea**

occulta, *Ornithoboea occulta* B.L.Burtt, Thailand, Tak, Mae Sot, 11 ix 2009, *D.J. Middleton, 4858*, (BK, BKF, E). ITS: *KU203838; *trnL-trnF*: *KU203933. **Ornithoboea pseudoflexuosa 1,** *Ornithoboea pseudoflexuosa* B.L.Burtt, Thailand, Surat Thani, Phanom, 26 ix 2010, *D.J. Middleton, 5545*, (BK, BKF, E). ITS: *KU203837; *trnL-trnF*: *KU203932; *ndhF-trnL*^{UAG}: *KU204006. **Ornithoboea pseudoflexuosa 2,** *Ornithoboea pseudoflexuosa* B.L.Burtt, Thailand, Surat Thani, Phanom , 7 ix 2008, *D.J. Middleton & al., 4336*, (BK, BKF, E). ITS: *KU203968; *trnL-trnF*: *KU204040; *ndhF-trnL*^{UAG}: *KU204007. **Ornithoboea puglisiae,** *Ornithoboea puglisiae* S.M.Scott, Thailand, Nan, Muang Nan, 16 viii 2012, *D.J. Middleton & al., 5617*, (BK, BKF, E). ITS: *KU203840; *trnL-trnF*: *KU203935. **Ornithoboea wildeana,** *Ornithoboea wildeana* Craib, Thailand, Chiang Mai, Doi Chiang Dao Wildlife Sanctuary, 20 ix 2008, *D.J. Middleton & al., 4531*, (BKF, E). ITS: JN934752; *trnL-trnF*: JN934710 *ndhF-trnL*^{UAG}: *KU204008. **Paraboea acutifolia 1,** *Paraboea acutifolia* (Ridl.) B.L.Burtt, Thailand, Satun, Manang, Phu Pha Phet Cave area, 10 ix 2010, *D.J. Middleton, 5365*, (BKF, E). ITS: *KU203867; *trnL-trnF*: *KU203962; *ndhF-trnL*^{UAG}: *KU204026. **Paraboea acutifolia 2,** *Paraboea acutifolia* (Ridl.) B.L.Burtt, Thailand, Krabi, Wat Tham Seua, 11 ix 2008, *D.J. Middleton, 4446*, (BK, BKF, E). ITS: *KU203969; *trnL-trnF*: *KU204041; *ndhF-trnL*^{UAG}: *KU204027. **Paraboea amplifolia,** *Paraboea amplifolia* Z.R.Xu & B.L.Burtt, Thailand, Trang, 30 viii 2009, *P. Triboun, s.n. (EDNA09_02281)*, (BK). ITS: JN934754; *trnL-trnF*: JN934712; *ndhF-trnL*^{UAG}: *KU204033. **Paraboea axillaris,** *Paraboea axillaris* Triboun, Thailand, Tak, Tah Song Yang District, 10 ix 2009, ex cult. RBGE 20092055, *D.J. Middleton, 4840*, (E). ITS: *KU203848; *trnL-trnF*: *KU203943. **Paraboea banyengiana,** *Paraboea banyengiana* B.L.Burtt, Malaysia, Sarawak, Gunung Mulu NP, 6 viii 2010, *C. Puglisi, CP 28*, (E). ITS: JN934755; *trnL-trnF*: JN934713. **Paraboea barnettiae,** *Paraboea barnettiae* C.Puglisi, Thailand, Peninsular Thailand, *K. Williams & al., 2118*, (A). ITS: *KU203847; *trnL-trnF*: *KU203942; *ndhF-trnL*^{UAG}: *KU204030. **Paraboea bhumiboliana,** *Paraboea bhumiboliana* Triboun & Chuchan, Thailand, Lamphun, Li, 9 ix 2009, *D.J. Middleton & P. Triboun, 4814G*, (E). ITS: JN934791; *trnL-trnF*: JN934749. **Paraboea birmanica,** *Paraboea birmanica* (Craib) C.Puglisi, China, Guangxi, Jing Xi, Nan Po, 1 ix 2006, *M. Möller & Y.G. Wei, MMO 06-862b*, (E). ITS: *KU203849; *trnL-trnF*:

*KU203944. **Paraboea brachycarpa,** *Paraboea brachycarpa* (Ridl.) B.L.Burtt, Malaysia, Pahang, Lipis distr., Gua Bama, *A. Weber, 870508-2/6*, (WU). ITS: *KU203870; *trnL-trnF*: *KU203965. **Paraboea brunnescens,** *Paraboea brunnescens* B.L.Burtt, Thailand, Kanchanaburi, Sisawat, Erawan National Park, 5 viii 2012, *D.J. Middleton & al., 5253*, (BK, BKF, E). ITS: *KU203859; *trnL-trnF*: *KU203954. **Paraboea burttii,** *Paraboea burttii* Z.R.Xu, Thailand, Phatthalung, Khao Banthat Wildlife Sanctuary, Khao Kram Waterfall, 13 ix 2010, *D.J. Middleton, 5407*, (BKF, E). ITS: *KU203858; *trnL-trnF*: *KU203953; *ndhF-trnL*^{UAG}: *KU204036. **Paraboea caerulescens,** *Paraboea caerulescens* (Ridl.) B.L.Burtt, Malaysia, Perak, Gunung Rapat, *FRIM, FRI 64604*, (KEP). ITS: *KU203871; *trnL-trnF*: *KU203966. **Paraboea capitata,** *Paraboea capitata* Ridl., Malaysia, Perak, *A. Weber, 870522-5/2*, (WU). ITS: FJ501315; *trnL-trnF*: AJ492298. **Paraboea capitata var. oblongifolia,** *Paraboea capitata* var. *oblongifolia* Ridl., Malaysia, Perak, Gua Tempurung, *FRIM, FRI 64598*, (KEP). ITS: *KU203861; *trnL-trnF*: *KU203956. **Paraboea clarkei,** *Paraboea clarkei* B.L.Burtt, Malaysia, Sarawak, Bau, Fairy cave, 17 vii 2010, *C. Puglisi, CP 10*, (E). ITS: JN934757; *trnL-trnF*: JN934715. **Paraboea crassifolia 1,** *Paraboea crassifolia* (Hemsl.) B.L.Burtt, China, Guangxi, Ma Shan, 24 viii 2006, *M. Möller & Y.G. Wei, MMO 06-804a*, (E). ITS: *KU203841; *trnL-trnF*: *KU203936; *ndhF-trnL*^{UAG}: *KU204016. **Paraboea crassifolia 2,** *Paraboea crassifolia* (Hemsl.) B.L.Burtt, China, Yunnan, Maguan, near Gulin Qing, 18 x 2001, *M. Möller & Y.D. Qi, MMO 01-83/2*, (E). ITS: JN934758; *trnL-trnF*: JN934716. **Paraboea crassifolia 3,** *Paraboea crassifolia* (Hemsl.) B.L.Burtt, China, Guizhou, Jiang Kou, 16 ix 2003, *M. Möller & L.M. Gao, MMO 03-322a*, (E). ITS: *KU203970; *trnL-trnF*: *KU204042; *ndhF-trnL*^{UAG}: *KU204017. **Paraboea divaricata,** *Paraboea divaricata* (Ridl.) B.L.Burtt, Thailand, Satun, La Ngu, Mu Ko Phetra National Park, 20 ix 2010, *D.J. Middleton, 5488*, (BKF, E). ITS: *KU203865; *trnL-trnF*: *KU203960; *ndhF-trnL*^{UAG}: *KU204034. **Paraboea doitungensis,** *Paraboea doitungensis* Triboun & D.J.Middleton, Thailand, Chiang Rai, Mae Fa Luang, Doi Tung, 23 ix 2008, *D.J. Middleton & al., 4576*, (BK, BKF, E). ITS: *KU203846; *trnL-trnF*: *KU203941; *ndhF-trnL*^{UAG}: *KU204020. **Paraboea eburnea,** *Paraboea eburnea* Triboun, Thailand, Ranong, Tham Pha Kayang, 31 vii 2009, *P. Triboun, s.n. (EDNA12_27741)*, (BK). ITS: *KU203869; *trnL-trnF*: *KU203964. **Paraboea effusa,** *Paraboea effusa*

B.L.Burtt, Malaysia, Sarawak, Mulu, 14 viii 2010, *C. Puglisi, CP 32*, (E). ITS: JN934760; *trnL-trnF*: JN934718. **Paraboea evrardii,** *Middletonia evrardii* (Pellegr.) C.Puglisi, Vietnam, Ninh Thuận PRO., Ninh Hải, 11 xi 2010, *Lý Ngọc Sâm & Phạm Vũ Điệp, Lý 497*, (E). ITS: *KU203790; *trnL-trnF*: *KU203885; *ndhF-trnL*^{UAG}: *KU203984. **Paraboea ferruginea,** *Paraboea ferruginea* (Ridl.) Ridl., Malaysia, Kedah, Pulau Langkawi, *A. Weber, 860806*, (WU). ITS: *KU203862; *trnL-trnF*: *KU203957. **Paraboea glabra,** *Paraboea glabra* (Ridl.) B.L.Burtt, Thailand, Krabi or Phangnga, *P. Triboun, s.n. (EDNA09_01765)*, (BK). ITS: JN934761; *trnL-trnF*: JN934719; *ndhF-trnL*^{UAG}: *KU204035. **Paraboea glabrescens,** *Paraboea glabrescens* (Barnett) C.Puglisi, Thailand, Kanchanaburi, Thong Pha Phum, 5 viii 2012, *D.J. Middleton & al., 5254*, (BK, BKF, E). ITS: *KU203852; *trnL-trnF*: *KU203947. **Paraboea glabrisepala,** *Paraboea glabrisepala* B.L.Burtt, Thailand, Chiang Mai, Doi Chiang Dao Wildlife Sanctuary, 20 ix 2008, *D.J. Middleton & al., 4533*, (BK, BKF, E). ITS: JN934762; *trnL-trnF*: JN934720. **Paraboea glanduliflora,** *Paraboea glanduliflora* Barnett, Thailand, Chiang Rai, Fang, Doi Ang Khang, 21 ix 2008, *D.J. Middleton & al., 4545*, (BK, BKF, E). ITS: JN934763; *trnL-trnF*: JN934721. **Paraboea glandulosa,** *Paraboea glandulosa* (B.L.Burtt) C.Puglisi, Thailand, Kanchanaburi, Thong Pha Phum , 28 x 2009, *D.J. Middleton & P. Triboun, 5202G*, (BK, E). ITS: JN934784; *trnL-trnF*: JN934742; *ndhF-trnL*^{UAG}: *KU204032. **Paraboea glutinosa,** *Paraboea glutinosa* (Hand.-Mazz.) K.Y.Pan, China, Guangxi, Xin Cheng, 23 viii 2006, *M. Möller & Y.G. Wei, MMO 06-786a*, (E). ITS: JN934764; *trnL-trnF*: JN934722; *ndhF-trnL*^{UAG}: *KU204025. **Paraboea harroviana var. ovata,** *Paraboea harroviana* (Craib) Z.R.Xu var. *ovata* Z.R.Xu, Thailand, Prachuap Khiri Khan, Khao Loom Muak, 5 ix 2008, *D.J. Middleton & al., 4273*, (BK, BKF, E). ITS: JN934765; *trnL-trnF*: JN934723; *ndhF-trnL*^{UAG}: *KU204021. **Paraboea havilandii,** *Paraboea havilandii* (Ridl.) B.L.Burtt, Malaysia, Sarawak, Bau, Tai Ton, 21 vii 2010, *C. Puglisi, CP18*, (E). ITS: JN934766; *trnL-trnF*: JN934724. **Paraboea hekouensis,** *Paraboea hekouensis* Y.M. Shui & W.H. Chen, China, Yunnan, Hekou, ix 2012, *Shui & al., 94842*, (KUN). ITS: *KU203843; *trnL-trnF*: *KU203938. **Paraboea incudicarpa,** *Paraboea incudicarpa* B.L.Burtt, Thailand, Tak, Mae Sot , 11 ix 2009, *D.J. Middleton & P. Triboun, 4857G*, (BK, E). ITS: JN934767; *trnL-trnF*: JN934725. **Paraboea insularis,** *Paraboea insularis* Triboun, Thailand, Krabi, Ao Luk, *P. Triboun, 3673*,

(BK). ITS: *KU203857; *trnL-trnF*: *KU203952. **Paraboea leuserensis,** *Paraboea leuserensis* B.L.Burtt, Indonesia, Sumatra, North Sumatra, 9 vii 2011, *C. Puglisi & al., CP 231*, (BO, E). ITS: *KU203863; *trnL-trnF*: *KU203958. **Paraboea longipetiolata,** *Paraboea longipetiolata* (B.L.Burtt) C.Puglisi, Thailand, Kanchanaburi, Thong Pha Phum, 6 viii 2012, *D.J. Middleton & al., 5257*, (BK, BKF, E). ITS: *KU203851; *trnL-trnF*: *KU203946. **Paraboea manhaoensis,** *Paraboea manhaoensis* Y.M. Shui & W.H. Chen, China, Yunnan, Gejiu, 7 ix 2012, *Shui & al., s.n. (EDNA13_30239)*, (KUN). ITS: *KU203842; *trnL-trnF*: *KU203937. **Paraboea middletonii,** *Paraboea middletonii* Triboun, Thailand, Nan, Doi Phu Kha National Park, 15 viii 2012, *D.J. Middleton & al., 5606*, (BK, BKF, E). ITS: *KU203845; *trnL-trnF*: *KU203940; *ndhF-trnL*^{UAG}: *KU204022. **Paraboea minor,** *Paraboea minor* (Barnett) B.L.Burtt, Thailand, Songkhla, Ton Nga Chang Wildlife Sanctuary, 7 ix 2010, *D.J. Middleton & al., 5225*, (BKF, E). ITS: *KU203860; *trnL-trnF*: *KU203955. **Paraboea monticola**, *Middletonia monticola* (Triboun & D.J.Middleton) C.Puglisi, Thailand, Surat Thani, Khlong Phanom National Park, 7 ix 2008, *D.J. Middleton & al., 4363*, (BK, BKF, E). ITS: *KU203789; *trnL-trnF*: KU203884; *ndhF-trnL*^{UAG}: *KU203982. **Paraboea multiflora,** *Middletonia multiflora* (R.Br.) C.Puglisi, Thailand, Sukhothai, Khiri Mat, 12 viii 2012, *D.J. Middleton & al., 5557*, (BK, BKF, E). ITS: *KU203791; *trnL-trnF*: *KU203886; *ndhF-trnL*^{UAG}: *KU203983. **Paraboea neurophylla,** *Paraboea neurophylla* (Collett & Hemsl.) B.L.Burtt, Thailand, Chiang Rai, Mae Fa Luang, 23 ix 2008, *D.J. Middleton & al., 4557*, (BK, BKF, E). ITS: JN934769; *trnL-trnF*: JN934727; *ndhF-trnL*^{UAG}: *KU204015. **Paraboea paniculata,** *Paraboea paniculata* (Ridl.) B.L.Burtt, Malaysia, *FRIM, FRI 65535*, (KEP). ITS: JN934770; *trnL-trnF*: JN934728; *ndhF-trnL*^{UAG}: *KU204039. **Paraboea paramartinii,** *Paraboea paramartinii* Z.R.Xu & B.L.Burtt, China, Guangxi, Napo, 1 ix 2006, *M. Möller & Y.G. Wei, MMO 06-852b*, (E). ITS: JN934771; *trnL-trnF*: JN934729. **Paraboea patens,** *Paraboea patens* (Ridl.) B.L.Burtt, Thailand, Phangnga, Phangnga Town Park, 17 ix 2010, *D.J. Middleton & al., 5456*, (BKF, E). ITS: *KU203864; *trnL-trnF*: *KU203959. **Paraboea peninsularis,** *Paraboea peninsularis* Triboun & D.J. Middleton, Thailand, Krabi, Ko Phi Phi National Park, 11 ix 2008, *D.J. Middleton & al., 4449*, (BK, BKF, E). ITS: JN934788; *trnL-trnF*: JN934746. **Paraboea phanomensis,** *Paraboea phanomensis* Triboun & D.J. Middleton, Thailand, Surat Thani, Khlong Phanom

National Park, 7 ix 2008, *D.J. Middleton & al., 4365*, (BK, BKF, E). ITS: *KU203855; *trnL-trnF*: *KU203950. **Paraboea rabilii,** *Paraboea rabilii* Z.R.Xu & B.L.Burtt, Thailand, Trang, Huai Yot, *P. Triboun, s.n. (EDNA11_02030)*, (BK). ITS: *KU203856; *trnL-trnF*: *KU203951. **Paraboea rosea,** *Paraboea rosea* Triboun, Thailand, Krabi, Talabeng Is., *P. Triboun, s.n. (EDNA09_02286)*, (BK). ITS: *KU203866; *trnL-trnF*: *KU203961; *ndhF-trnL*^{UAG}: *KU204037. **Paraboea rufescens,** *Paraboea rufescens* (Franch.) B.L.Burtt, China, Yunnan, 19 x 2001, *M. Möller & Y.D. Qi, MMO 01-108/3*, (E). ITS: JN934772; *trnL-trnF*: JN934730. **Paraboea rufescens var. tomentosa,** *Paraboea rufescens* var. *tomentosa* (Barnett) Z.R.Xu, ex cult RBGE 20091920, *C. Puglisi*, (E). ITS: *KU203971; *trnL-trnF*: *KU204043; *ndhF-trnL*^{UAG}: *KU204023. **Paraboea sangwaniae,** *Paraboea sangwaniae* Triboun, Thailand, Chiang Rai, Mae Fa Luang, 23 ix 2008, *D.J. Middleton & al., 4572*, (BK, BKF, E). ITS: JN934787; *trnL-trnF*: JN934745. **Paraboea siamensis,** *Paraboea siamensis* Triboun, Thailand, Tak, Umphang, 7 ix 2010, *P. Triboun & al., 4565*, (BK, BKF, E). ITS: *KU203853; *trnL-trnF*: *KU203948. **Paraboea sinensis,** *Paraboea sinensis* (Oliv.) B.L.Burtt, China, Yunnan, Hekou, 20 ix 2006, *M. Möller & L.M. Gao, MMO 06-949a*, (E). ITS: *KU203844; *trnL-trnF*: *KU203939; *ndhF-trnL*^{UAG}: *KU204024. **Paraboea subplana,** *Paraboea subplana* (B.L.Burtt) C.Puglisi, Thailand, Krabi, Wat Tham Seua, 11 ix 2008, *D.J. Middleton, 4444*, (BK, BKF, E). ITS: *KU203854; *trnL-trnF*: *KU203949; *ndhF-trnL*^{UAG}: *KU204031. **Paraboea suffruticosa,** *Paraboea suffruticosa* (Ridl.) B.L.Burtt, Thailand, Satun, Mu Ko Phetra National Park, 10 ix 2008, *D.J. Middleton & al., 4432*, (BK, BKF, E). ITS: JN934774; *trnL-trnF*: JN934732. **Paraboea swinhoei,** *Paraboea swinhoei* (Hance) B.L.Burtt, China, Guangxi, Xin Cheng, 23 viii 2006, *M. Möller & Y.G. Wei, MMO 06-783c*, (E). ITS: JN934775; *trnL-trnF*: JN934733. **Paraboea tarutaoensis,** *Paraboea tarutaoensis* Z.R.Xu & B.L.Burtt, Thailand, Satun, ex cult. RBGE 20082069, *D.J. Middleton*, (E). ITS: JN934776; *trnL-trnF*: JN934734. **Paraboea trachyphylla,** *Paraboea trachyphylla* Z.R.Xu & B.L.Burtt, Thailand, Surat Thani, Ban Thakhun , 6 ix 2008, *D.J. Middleton & al., 4310*, (E). ITS: JN934777; *trnL-trnF*: JN934735; *ndhF-trnL*^{UAG}: *KU204028. **Paraboea treubii,** *Paraboea treubii* (H.O.Forbes) B.L.Burtt, Indonesia, Sumatra, North Sumatra, 11 vii 2011, *C. Puglisi & al., CP 275*, (BO, E). ITS: *KU203872; *trnL-trnF*: *KU203967. **Paraboea trisepala,**

Paraboea trisepala W.H.Chen & Y.M.Shui, China, Guangxi Jing Xi, *Y.M. Shui & al., CH 153*, (KIB). ITS: JN934778; *trnL-trnF*: JN934736. **Paraboea umbellata,** *Paraboea umbellata* (Drake) B.L.Burtt, China, Guangxi, Napo, 22 x 2001, *M. Möller & Y.D. Qi, MMO 01-147/2*, (E). ITS: JN934779; *trnL-trnF*: JN934737; *ndhF-trnL*^{UAG}: *KU204019. **Paraboea variopila,** *Paraboea variopila* Z.R.Xu & B.L.Burtt, Thailand, Nakhon Si Thammarat, Thung Song, 11 ix 2010, *D.J. Middleton & al., 5392*, (BK, BKF, E). ITS: *KU203868; *trnL-trnF*: *KU203963 (partial); *ndhF-trnL*^{UAG}: *KU204029. **Paraboea velutina,** *Paraboea velutina* (W.T.Wang & C.Z.Gao) B.L.Burtt, China, Guangxi, Feng Shan, 4 vi 2007, *M. Möller & Y.G. Wei, MMO 07-1105a*, (E). ITS: JN934780; *trnL-trnF*: JN934738; *ndhF-trnL*^{UAG}: *KU204018. **Paraboea verticillata,** *Paraboea verticillata* (Ridl.) B.L.Burtt, Malaysia, Selangor, *FRIM, FRI 48225*, (KEP). ITS: JN934781; *trnL-trnF*: JN934739; *ndhF-trnL*^{UAG}: *KU204038. **Paraboea vulpina,** *Paraboea vulpina* Ridl., Thailand, Krabi, Muang Krabi, 11 ix 2008, *D.J. Middleton & al., 4442*, (E). ITS: JN934782; *trnL-trnF*: JN934740. **Paraboea xylocaulis,** *Paraboea xylocaulis* Triboun, Thailand, Krabi, Ao Luk, P. *Triboun, 3674*, (BK). ITS: JN934789; *trnL-trnF*: JN934747. **Rhabdothamnopsis sinensis 1,** *Rhabothamnopsis sinensis* Hemsl., China, Yunnan, Zhao Tong, 22 vii 2010, *M. Möller & P. Zhou, MMO 10-1667A*, (E). ITS: *KU203829; *trnL-trnF*: *KU203924. **Rhabdothamnopsis sinensis 2,** *Rhabothamnopsis sinensis* Hemsl., China, Sichuan, Luding, 17 viii 2009, *M. Möller & P. Zhou, MMO 09-1613*, (E). ITS: *KU203828; *trnL-trnF*: *KU203923. **Rhabdothamnopsis sinensis 3,** *Rhabothamnopsis sinensis* Hemsl., China, ex cult. RBGKew 19884866, (K). ITS: JN934794; *trnL-trnF*: AJ492302. **Senyumia minutiflora,** *Senyumia minutiflora* (Ridl.) Kiew, A.Weber & B.L.Burtt, Malaysia, Pahang, *A.R. Rafidah, 55722*, (KEP). ITS: HQ632957; *trnL-trnF*: HQ632865; *ndhF-trnL*^{UAG}: *KU203999. **Somrania albiflora,** *Somrania albiflora* D.J.Middleton, Thailand, Ranong, Kra Buri, 16 viii 2006, *K. Williams & al., 2123*, (A, BKF). ITS: *KU203792; *trnL-trnF*: *KU203887; *ndhF-trnL*^{UAG}: *KU203987. **Somrania flavida,** *Somrania flavida* D.J.Middleton & Triboun, Thailand, Surat Thani, Khao Sok, *D.J. Middleton & al., 4324*, (E). ITS: *KU203794; *trnL-trnF*: *KU203889; *ndhF-trnL*^{UAG}: *KU203988. **Somrania lineata,** *Somrania lineata* D.J.Middleton & Triboun, Thailand, Phangnga, Muang Phangnga, Tham Pha Phueng, 15 ix 2010, *D.J. Middleton & al., 5434*, (BKF, E). ITS: *KU203793; *trnL-*

trnF: *KU203888; *ndhF-trnL*^{UAG}: *KU203989. **Spelaeanthus chinii 1,** *Spelaeanthus chinii* Kiew, A.Weber & B.L.Burtt, Malaysia, Pahang, Jerantut distr., *A. Weber, 860709-2/2*, (WU). ITS: FJ501307; *trnL-trnF*: FJ501457;. **Spelaeanthus chinii 2,** *Spelaeanthus chinii* Kiew, A.Weber & B.L.Burtt, Malaysia, Peninsular Malaysia, 27 viii 2008, *R. Kiew, FRI 60061*, (KEP). ITS: *KU203807; *trnL-trnF*: *KU203902; *ndhF-trnL*^{UAG}: *KU203998. **Streptocarpus glandulosissimus,** *Streptocarpus glandulosissimus* Engl., Tanzania, ex cult. RBGE 19652118, *O.M. Hilliard, S10*, (E). ITS: AF316918; *trnL-trnF*: *KU203874; *ndhF-trnL*^{UAG}: *KU203972. **Streptocarpus orientalis 1,** *Damrongia orientalis* (Craib) C.Puglisi, Thailand, Sukhothai, Khiri Mat, 12 viii 2012, *D.J. Middleton & al., 5561*, (BK, BKF, E). ITS: *KU203795; *trnL-trnF*: *KU203890; *ndhF-trnL*^{UAG}: *KU203990. **Streptocarpus orientalis 2,** *Damrongia orientalis* (Craib) C.Puglisi, Thailand, 22 vii 2002, *EDNA12_27733*, (E). ITS: *KU203796; *trnL-trnF*: *KU203891. **Streptocarpus orientalis 3,** *Damrongia orientalis* (Craib) C.Puglisi, Thailand, Chiang Mai, *P. Palee, s.n. (EDNA08_01210)*, (E). ITS: *KU203797; *trnL-trnF*: *KU203892. **Streptocarpus rexii,** Streptocarpus rexii (Bowie ex Hook.) Lindl., South Africa, Grahamstown, 'Faraway' estate, 29 x 1986, ex cult. RBGE 19870333, *K. Jong s.n.*, (E). ITS: AF316979; *trnL-trnF*: AJ492305; *ndhF-trnL*^{UAG}: *KU203973. **Streptocarpus sumatranus,** *Damrongia sumatrana* (B.L.Burtt) C.Puglisi, Indonesia, Sumatra, West Sumatra, 24 vi 2011, *C. Puglisi & al., CP 127*, (BO, E). ITS: *KU203800; *trnL-trnF*: *KU203895; *ndhF-trnL*^{UAG}: *KU203992.